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Some biological interactions of Empoasca phaseola Oman (Homoptera:Cicadellidae) with selected leguminous hosts

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Some biological interactions of Empoasca phaseola Oman (Homoptera:Cicadellidae) with selected leguminous hosts

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INTRODUCTION

As with all phytophagous insects, both the numbers and distribution of Empoasca phaseola Oman are significantly regulated by the degree of their acceptance and utilization of specific host plants. Further regulation of insect numbers may be imposed by the influence of host plant qualities upon the insect's reproductive rate. The investigations reported in this dissertation were undertaken to provide knowledge of host plant influence upon the reproduction of E. phaseola, a little known but economically threatening pest of beans in Central America.

The significance of leafhoppers of the genus Empoasca as pests of cultivated beans, thus far disregarded, was clearly demonstrated during a routine visit of experimental plots in the Guanacaste Peninsula of Costa Rica. Exploratory ventures at that site were part of a development program sponsored by the Interamerican Institute of Agricultural Sciences and aimed at reinstating the common bean, a basic food item, in the ecological regions best suited to its production. Within the research scheme, Guanacaste figured as a marginal testing zone and was expected to foster a high incidence of pests and diseases. Plantings there included several hundreds of cultivars.

The great majority of the plants were severely affected; they were stunted and the leaves were curled and yellowed. The suggestion that these unusual features could be caused by leafhoppers which abounded in the fields was endorsed with hesitation. Indeed, the symptoms could be attributed to several other causes such as lack of moisture, mineral

deficiencies, and fungus or virus infections. Nevertheless, in view of the extent of the damage, a research program was authorized. In consultation with Dr. Edwin T. Hibbs of Iowa State University, plans were developed for the collection of data dealing with a species of Empoasca, thus far little studied. The program was launched and carried out continuously during three years.

It should, perhaps, be added that the importance of Cicadellidae revealed in Costa Rica is in fact a pest problem of beans throughout Central America and the present study is applicable to most of that region. For practical purposes, however, the accounts herein refer particularly to Costa Rica, which is broadly representative of the whole geographical area from the viewpoints of topography, climate, fauna and flora, agricultural practices, and dietary habits of its human inhabitants.

Common bean (Phaseolus vulgaris L.) and related legumes have long been staple crops in the area and are, in the present, widely planted either as homestead gardens or large commercial stands. Liberal imports of Phaseolus stocks have introduced cultivars which are susceptible to the pest. In addition, scores of indigenous hosts carry dense populations of E. phaseola through the dry periods when the rain-dependent food crops are not present. These wild species are often allowed to grow to tree size and represent standard components of the farmstead, either as live posts or ornamental shrubs.

The dazzling variations in the ecological pattern of Central America, largely due to the tormented relief, lead to a great diversity of climate

and allow local movements of insects among suitable contiguous habitats, assuring their survival or reproduction throughout the year. Within this subtly interwoven complex of climate, insect dispersals, and distribution of host species favored by climate and cropping practices, E. phaseola has kept itself proliferating in bean fields during the rainy season and maintaining its level of abundance the rest of the time on less favorable, but always present, host species.

LITERATURE REVIEW

Geography and Climate of Central America

Central America represents a narrow band of continental land extending out in a general north-west south-east direction. The total area, from Mexico to Colombia, is (according to G. Ordish (1964)) but one-twentieth of the size of North America. Once a single Spanish colony, the region from southern Mexico to Panama is now divided into five small independent countries (thus excluding British Honduras): Guatemala, Honduras, Salvador, Nicaragua and Costa Rica.

The Central American area is typically mountainous. The topography is dominated by the Central Plateau (La Meseta Central), which runs along the long axis of the stretch of land and varies in altitude from about 1,000 to 2,000 meters (Fig. 1). From this median highland area, the territory slopes down toward the Pacific Ocean to the west, the Caribbean Sea to the east and is towered by a high cordillera made up of a succession of volcanic peaks.

All of Central America is located in the tropical zone, but the region offers considerable climatic diversity from place to place. Basically, the longitudinal middle range shields the Pacific slope from the dominant trade winds, causing this slope to be generally dry, but receiving rains at definite periods. The Atlantic slope receives the moisture from the ocean and is, in contrast, exceedingly humid with an annual rainfall of up to 4 meters. On either side of the isthmus, temperatures are high along the coast and decrease gradually with increasing elevation.

The vegetation varies with the climate. The humid eastern slope is largely tropical rain forest disrupted with some economic crops like cacao, banana, and sugarcane. The fertile Central Plateau is the real agricultural area and is planted extensively in food crops and fruit trees (Fig. 2). As the terrain rises, coffee is largely found with occasional patches of wheat, barley, vegetables, and corn. The volcanic peaks are either bare or covered with a mixture of conifers and hardwood tree species.

The foregoing is naturally very broad and sketchy. In fact, the interweaving of an irregular topography, the latitude, and oceanic influences impart to the region a mosaic-like bioclimatic pattern which L. R. Holdridge (1968) has rationalized through a classification as "life-zones". He coined names for his "life-zones" according to climatic, edaphic, and topographical factors e.g. "Premontane Wet Forest", "Premontane Moist Forest", "Tropical Dry Forest", "Moist Province Transition", etc. An adaptation of Holdridge ecological map is given in Figs. 3 and 4.

Description of Empoasca phaseola Oman

Empoasca phaseola was initially described by P. W. Oman (1936). The species is comparatively large (being about 4.25 mm long), slender, pale green to yellowish green with a few individuals being a definite azure. Some ill-defined white markings can be seen on head and thorax. The front wings often show faint golden longitudinal stripes. The lateral processes of the male genitalia are stout, straight basally, sinuated apically, the tips being enlarged and foot-shaped.

The original description by P. W. Oman was made from specimens collected at San Pedro de Monte de Oca, a locality of the Central Plateau of Costa Rica, about 1,300 meters high.

Phylogenetically, there seems to be a question as to where the species should be located. D. A. Young (1956) stated that it is of "uncertain position." H. H. Ross (1956) did not include it in his survey of the Empoasca fabae complex. H. B. Cunningham (1962), in his revision of the genus Empoasca, placed it as a branch of the species muricata, itself an early offshoot of junipera, one of the three monophyletic groups of the fabae line.

From the phylogenetic tree of the subgenus Empoasca (Fig. 5), worked out by H. B. Cunningham (1962), it appears that the branch of muricata topped by phaseola may have undergone little change, while kraemeri branched off considerably giving rise to several species likely to adapt to a wide range of environmental conditions. This would be in accord with that which was observed in Central America and will be further stressed later. The fact might be added that since phaseola is limited to humid areas, that species is not adaptable to dry conditions. From the work of H. H. Ross, G. C. Decker and H. B. Cunningham (1965) it seems possible that such an adaptability may have played a differential role in the migration of Empoasca lineages from the neotropical to the temperate area and can explain the present stringent distribution of the species phaseola.

Bionomics of Empoasca leafhoppers

In a recent publication, D. M. DeLong (1971) reviewed the bionomics of Cicadellidae with abundant reference to Empoasca fabae Harris. His

special emphasis of this species is only natural, since the potato leafhopper, as it is commonly called, is an economic pest of many vegetable, fruit, and forage crops such as garden beans, celery, rhubarb, radish, apple, strawberry, watermelon, alfalfa, clover, etc. (F. F. Smith and F. W. Poos 1931; R. L. Wallis 1962).

E. fabae is a New World species known to be restricted in the North American continent within which it migrates each year in April and May from its breeding grounds in the Mississippi Valley to the mid-central and eastern regions. The annual northward migration would terminate at the junction point of the warm air masses from the south with the cooler masses of the northern states associated with the rainstorms of early spring (F. H. Huff 1963; R. L. Dienkowski and J. T. Medler 1964).

Homopterans of the family Cicadellidae characteristically live in close association with their plant hosts which supply them with food, shelter, and an appropriate site for living, mating, and depositing eggs.

Feeding

The feeding habits of cicadellids have been studied by a number of investigators, namely F. F. Smith and F. W. Poos (1931), and K. M. Smith (1926). Some species limit their feeding to the spongy mesophyll, some cells of which are emptied of their content. The cell walls of the palisade layer, which is traversed by the stylet-like mouth parts of the insect, are torn and the mesophyll displays multiple discolored circular areas, about 10 to 15 cells in diameter, or blotches, when the groups of damaged cells become confluent (A. S. Horne and H. M. Lefroy

1915). According to these authors, the loss of coloration would be due to the disappearance of chlorophyll from the cells and perhaps an optical effect resulting, in part, from the presence of air. K. M. Smith (1926) expressed the view that in the process of leafhopper feeding, groups of adjacent cells are emptied of their chlorophyll and partially collapse. The symptom of damage by these insects is expressed superficially as a stippling, more or less coarse, depending on the species. A central green dot is usually present within the white specks on account of the fact that the insect beak does not penetrate the plant tissues at right angles, but obliquely, and probes the cells in all directions from a central feeding point.

Another group of Cicadellidae, among which are E. fabae and E. phaseola, would feed mostly on phloem tissue, rupturing or distorting the cell layers. An encasing gelatinous sheath would be produced as a result of salivary emission which accompanies the sucking of plant sap and would be, according to F. F. Smith (1933), made up of protein or of a pectinate substance. The sheathing material would actually seal off the cells external to the phloem (C. W. Bennett 1934). The external signs of this second mode of feeding would be the stunting of the growing plants, curling or rolling under of the leaves (combined with an unusual roughening), crinkling or rugose appearance of the leaf tissue, and eventually various degrees and patterns of yellowing of the foliage. At this point it appears pertinent to add that F. F. Smith and F. W. Poos (1931) observed that the damage caused by E. fabae is extremely localized, affecting only that part of the plant beyond the point of feeding,

whether the damage is manifested as wilting, yellowing, or reddening. This seems to bar a systemic action of whatever substance is present in the salivary injection of the phloem feeders.

The sequence of symptoms brought about by these leafhoppers feeding on vascular tissue does not seem to be clearly understood and proposed hypotheses fall into two separate categories.

The first can be identified with A. A. Granovsky (1930), F. F. Smith and F. W. Poos (1931), and H. W. Johnson (1934), who claim that water and nutrients are not normally translocated to areas beyond the point of attack by the insect, due to the plugging of xylem tubes and the disruption of the phloem cells. Histological studies and microchemical tests by A. A. Granovsky (1930) showed an unusual accumulation of starch and of the sugars, glucose and fructose, within the affected areas; the plastids were found to be disorganized and granulated, clogging and isolating the vascular bundles. However, J. R. Eyer (1922), F. A. Fenton (1921), F. A. Fenton and I. L. Ressler (1922), in a series of ingenious experiments using fine sterilized needles, showed that the mechanical disruption of vascular tissues alone or the introduction into the plant of liquid mixtures of various compositions did not induce the typical leafhopper damage, commonly referred to as "hopperburn".

The second hypothesis, held by W. C. Carter (1939), J. T. Medler (1941), L. M. Black and P. A. Oman (1947), proposes that in the process of feeding, a toxic substance is injected by the insect. Leafhoppers do excrete enzymes as they feed. The function of these substances is probably multiple. It seems established that, in some cases, a form of

predigestion of carbohydrates takes place, the complex sugars being converted to simpler ones more easily utilizable by the organism. Under conditions of heavy leafhopper activity, an abnormal concentration of sugars can indeed be observed, as documented by A. H. Beyer (1922), who claims that the injection of amylase and invertase leads to the reduction of polysaccharides and that the release of plant hormones by the damaged phloem cells elicits starch hydrolysis. Whether or not substances capable of different enzymatic action are present in the saliva of leafhoppers is apparently not yet established.

J. T. Medler (1941) is of the opinion that both the physical and chemical effects combine to produce the physiological disturbances in the host plant. According to him, and as reported by D. M. DeLong (1971), "the salivary secretion causes hypertrophy of the affected phloem cells which, in turn, causes an interruption of the translocation of the photosynthetic materials from the leaves to a degree that causes plasmolysis of parenchymal cells and the resulting hopperburn." The damage inflicted to legumes, at least in its latest stages, somewhat recalls hopperburn on potatoes and offers, perhaps, a clearer development pattern. It is believed that the mechanism involved in the production of hopperburn may be elucidated by more detailed study of the damage of leafhoppers to common bean, Phaseolus vulgaris L., particularly.

According to G. E. Marshall and N. F. Childers (1942), injured apple leaves permanently lose their capacity to transpire and carry out photosynthesis. More recently, T. L. Ladd, Jr. and W. A. Rawlins (1965)

determined that photosynthesis and respiration were severely altered in plant tissues under heavy attack by E. fabae. E. T. Hibbs, D. L. Dahlman, and R. L. Rice (1964) found that tolerant and susceptible varieties of potatoes displayed sugar concentrations progressively greater from terminal to basal foliage, the sugar content being normally higher in the susceptible. These workers recorded their highest increase in sugar concentration in the physiologically aged lower leaves of susceptible stock, which was also most prone to develop necrosis, dry up and die.

The specific toxin in the salivary secretion of Cicadellidae, postulated by the contenders of the chemical causation of leafhopper damage, would not be a poison in the strict sense, but would be indirectly detrimental to the host in its effect on carbohydrate metabolism, provoking the "congestion" of sugars in the plant tissues, as expressed by H. W. Johnson (1934).

A complicating factor is naturally the voluminous intake of liquid food by leafhoppers (J. L. Auclair 1961, 1963), making it necessary to expel the apparent excess in the form of honeydew. Here again it is undecided whether the carbohydrates are simply flushed through the system or whether they have to undergo some metabolic process. V. G. Dethier and M. V. Rhoades (1954) devised an efficient method to determine the exact quantity of soluble material imbibed by insects. Sugars vary considerably in their survival value, some being inert, some of relatively low value as source of carbon, some fully capable of supporting life, and some interfering with those sugars normally well utilized.

Comparing the composition of the plant sap with that of the honeydew expelled by the feeding insect, F. Duspiva (1954), cited by H. Lipke and G. Fraenkel (1954) and H. E. Gray and G. Fraenkel (1954) arrived at the conclusion that following transglycosidation in the insect gut, the sugars of the plant sap are digested and metabolized. Concerning the volume of fluid thus processed, H. Lipke and G. Fraenkel (1954) point out the especially high requirement of homopterans for nitrogen on account of their high level of fecundity. It is thus plausible that the insects must ingest large volumes of liquid food to obtain essential amino acids and proteins (J. L. Auclair, J. B. Maltais and J. J. Cartier 1961). E. C. Albritton (1955) lists no less than 10 amino acids as being essential and 7 non-essential.

Cicadellidae are presumably no exception in requiring sterols in their diet. A. Koch, cited by H. Lipke and G. Fraenkel (1954) claims a paucity of vitamins in the cellular sap. The requirements of insects in both sterols and vitamins would be assured by the action of symbiotic yeasts.

Moisture and temperature requirements

Besides food, the plant host offers to leafhoppers an adequate living site and a shelter against adverse conditions of weather and physical environment. Humidity is a critical factor in the maintenance of homopterans, the diets of which are essentially liquid. F. H. Harries and J. R. Douglass (1948) and D. M. DeLong (1971) reported that Cicadellidae are unable to survive for long periods in the absence of

an abundant supply of cell sap or of an adequate fluid. Leafhoppers feed continuously and are anatomically equipped to handle large volumes of liquids. N. P. Metcalf and H. Osborn (1920) and D. M. DeLong (1971) cite the cases of leafhoppers associated with tidal submergence. Commonly, the entire life cycle of Cicadellidae is spent in a highly humid atmosphere. The eggs are inserted in leaf tissues or tender stems within which they incubate in a saturated environment. The nymphs spend most of their time on the underleaf, where the large majority of the stomata are located. Transpiration from the leaves creates, close to the foliar area, a highly moist microclimate suitable for the maintenance of the insects in dry to arid areas. The leaf blade, on the other hand, shields the delicate organisms against the desiccating action of direct exposure to sun rays. F. H. Harries and J. R. Douglass (1948) claim that leafhoppers die of lack of moisture during certain winters.

Extremely heavy rains may prevent the building up of large populations of leafhoppers, but are not as devastating as deficient precipitation. D. M. DeLong (1938) emphasizes the importance of an adequate distribution of rain showers during the growing season of the host plant. He cites the striking example of the year 1930, in which, because of an unusually low humidity, no record was made of Cicadellidae on any crop in Ohio, whilst, in normal years, this state is severely infested.

Empoascan leafhoppers require for their survival a high level of atmospheric moisture. D. M. DeLong (1938) explains the distribution

of E. fabae in the North American continent largely on the basis of a high relative humidity in the eastern and low in the western side of a dividing line situated at 40% relative humidity. This author further shows that if rainfall-evaporation ratio is used instead of relative humidity, the distribution is found to be roughly the same as when determined by climographs. It may not be superfluous to point out that rainfall-evaporation ratio is determined not only by rainfall but also by relative humidity, temperature, and wind velocity and is considered by certain authors, namely, E. N. Transeau (1905), B. E. Livingston and F. Shreve (1921), as a prime indicator of the distribution of plants and the insects which live on them.

Temperature alone is not known to be a limiting factor if it does not fall to levels below the freezing mark.

Mating and oviposition

Reproduction in leafhoppers is bisexual and mating is apparently required for the production of viable eggs. Parthenogenesis is known to occur, however, as in the case of the genus Agallia, reported by P. W. Oman (1949) with exclusive production of female progeny.

As a rule the mating process follows a distinct behavioral pattern in which the production of sounds is involved. According to F. Ossiannilsson (1949), enticing songs are emitted by the males and if the females answer with inviting songs, mating usually takes place. A typical dance will accompany the male courtship calls. This action of

transmitting substrate vibrations is interpreted by R. R. Perkes (1969) as a possible way of sexual communication.

Mating and oviposition of E. fabae were studied in considerable detail by O. V. Carlson (1967), who identified one male call as a stimulus for mate-identification at close range, poorly reinforced since male-to-male contacts were frequent as well as male attempts to copulate with mating pairs and female escapes.

According to the same author, females 3 days old could mate successfully and matings for females as old as 120 days old were recorded. While one mating is considered adequate to assure the fertilization of all the eggs produced by a female during her lifetime, he observed females mating as often as twice. Males 2 days old could copulate and would still be sexually active after 90 days; they copulated with several females. The average duration of the mating process was 84 minutes.

Oviposition is accomplished by inserting the sharp, curved ovipositor beneath the plant epidermis and cutting a cell in the underlying tissues. Within this cavity a single egg is deposited. The process is repeated over and over as long as the site is still appropriate, i.e. of appropriate physiological age. Neither very young nor senescent tissue seems to be used for oviposition. R. L. Miller and E. T. Hibbs (1953) determined that the median section of growing potato plants received the majority of the eggs, consistently in higher numbers in the single terminal leaflet than in the subterminal leaflet pairs of the axillary branches.

During the lifetime of a female leafhopper, and depending on the suitability and condition of the plant host, the total number of eggs deposited would vary from a few to a maximum of about 200. The oviposition period would last from 2 to 3 months. D. M. DeLong (1971) claims the average daily oviposition of E. fabae to be 2.7 eggs.

Incubation period and nymphal eclosion

The incubation period would vary with the conditions prevailing in the environment; the usual duration is from 8 to 10 days. The nymph at the end of the incubation period is enclosed in the chorion and vitelline membrane (H. H. P. Severin 1949). To emerge, it must push itself out of the slitlike opening of the egg chamber. Usually, it will free the anterior part of its body first, the abdomen still remaining in the embryonic envelope. Many do not succeed in escaping and die in that position. Newly emerged nymphs are delicate, unpigmented, and soft. They often fall to the ground and, according to H. H. P. Severin (1949), will survive by sipping moisture from the soil surface. In most cases, however, the first instar nymph will free itself from the plant tissues and immediately take refuge under the neighboring leaf blade.

OBSERVATIONS AND EXPLORATORY TRIALS

Collection of Empoasca

The first phase of my research on Central American Cicadellidae involved basic information on their taxonomic p sition, distribution and bionomics. During the three years of research, collections were made repeatedly at a great diversity of sites. The specimens were identified with the assistance of systematists of outstanding experience in that group of insects. Their determinations indicated that several species of Empoasca occur in the bean fields and on some common wild hosts, possibly with a predominance of E. kraemeri and E. phaseola. These species seem to distribute themselves in rather close correlation with the moisture gradient, kraemeri being mostly found in the dry locations and phaseola in the humid. Other Empoasca species of some significance were found to be prona, fabalis, abrupta, and erigeron. Many specimens could not be named and were simply identified as belonging to large species complexes. Figure 6 shows where the different species were collected. Table 1 relates elevation and rainfall at stations nearest to the actual collection sites, specifies the suitability of these sites for bean culture, and indicates the life zone of Holdridge's ecological map. This last information is intended as a gross approximation to actual moisture indicators which require abundant and varied meteorological records, which, unfortunately, are not always available on account of the great diversity of the bioclimate of the region and the limited number of weather stations.

Where there is an alternation of dry and wet seasons, the two

Table 1. Distribution of Empoasca on common bean (Phaseolus vulgaris L.) in Central America

Country	Locality	Altitude (m.)	Rainfall (mm.)	Suitability for bean production	Species encountered	Life zone (Holdridge)
COSTA RICA	Turrialba	600	3,500	Not suitable	E. phaseola[a]	Premontane moist forest
	Paraiso	1,450	2,000	Not suitable	E. phaseola[a]	Premontane moist forest
	Cervantes	1,375	2,000	Not suitable	E. kraemeri, phaseola, arator[b]	Subtropical very wet forest
	San Antonio	800	1,500	Very suitable	E. kraemeri, phaseola, arator[b]	Subtropical rain forest
	Canas	100	1,000	Suitable	E. kraemeri, arator[b]	Tropical dry forest, moist province transition
	Alajuela	1,200	2,000	Very suitable	E. kraemeri[a], arator[b], phaseola	Subtropical humid forest
	Liberia	300	1,750	Very suitable	E. kraemeri[a], arator	Premontane moist forest, basal belt transition
	San Isidro del General	-	2,500	Very suitable	E. kraemeri[a]	Tropical moist forest
	Cartago	2,300	2,500	Suitable	E. phaseola[a]	Premontane moist forest
NICARAGUA	Matagalpa	900	1,300	Very suitable	E. kraemeri, arator, phaseola[b]	Tropical dry forest, moist province
	Somoto	750	1,250	Suitable	E. kraemeri[a]	Tropical dry forest
	Esteli	900	1,000	Very suitable	E. kraemeri, arator	Tropical dry forest

[a]Numerically more abundant or exclusive.

[b]Abundant.

Table 1. (continued)

Country	Locality	Altitude (m.)	Rainfall (mm.)	Suitability for bean production	Species encountered	Life zone (Holdridge)
EL SALVADOR	San Andres	500	1,800	Suitable	E. kraemeri[a], phaseola[b]	Subtropical wet forest
	Apopa	600	2,000	Suitable	E. kraemeri, phaseola	Tropical dry forest
GUATEMALA	Las Moritas	500	2,100	Very suitable	E. kraemeri[a], phaseola[b]	Tropical dry forest, moist province transition
	Jutiapa	900	2,000	Very suitable	E. kraemeri[a], phaseola[b], arator	Subtropical dry forest
	Chimaltenango	1,950	1,500	Not suitable	E. phaseola[a], kraemeri	Premontane wet forest
HONDURAS	Danli	800	1,400	Very suitable	E. kraemeri, phaseola	Subtropical wet forest
	Zamorano	-	800	Suitable	E. kraemeri, phaseola	Subtropical dry forest

numerically more abundant species, kraemeri and phaseola, constituted mixed populations and contained small numbers of the less predominant species. In the highlands going up toward the volcanic peaks, phaseola gradually replaced kraemeri up to a point where the host plants of leafhopper populations are no more encountered. In Guatemala, phaseola was found rather abundantly in some scattered bean patches, as high as 2,000 meters.

Oviposition on Native Plant Species

A cursory survey was made of the most common plant species growing spontaneously on or near farmsteads to determine whether they were used as hosts by empoascan leafhoppers. Acnistus arborescens Schlechtd., locally called "huitite", Cestrum warscewiczii Klotzsch, an ornamental shrub, Rollinia and Dahlia, species of which are either grown as ornamentals or found in the wild state, volunteer potato plants (Solanum tuberosum L.), were examined for damage to the foliage or presence of eggs.

Both Acnistus and Cestrum were heavily infested (Figs. 7 and 8). These species are used as live posts or hedges and obviously represent reservoirs of outstanding importance. Rollinia and Dahlia are not as widespread and probably are of lesser significance in the maintenance of populations of the leafhoppers. It was surprising that potato, although growing among common bean plants, themselves severely attacked, showed no sign of damage and no eggs were located in the leaves and sections of stems.

The search for wild hosts was not pursued any further although in the extreme diversity of tropical plants, a great many more species must serve as hosts to Empoasca leafhoppers.

Life History Study of Captive E. phaseola

This second phase of the program was conducted at the Turrialba Research Center in Costa Rica. This station is located on the Pacific slope, at an elevation of 600 meters. The basic plan was to develop captive populations which could be manipulated according to needs.

The first colonies to be established were of E. phaseola from individuals collected on a wild solanaceous plant Cestrum warscewiczii Klotzsch at Cartago, Costa Rica, on the Central Plateau, at an altitude of 2,300 meters (Fig. 8). From previous determinations, chances were that the population would be pure and not a mixture of species. Periodic samplings at that site showed that the conditions were undoubtedly favorable as evidenced by an ever-present dense population of E. phaseola. The natural population as well as the captive one at the Research Center were frequently checked for purity. Reference specimens, dry on points, were deposited with the Iowa Insect Collection.

Soon it was established that oviposition would occur in captivity on common bean. Other related plant species such as lima bean (Phaseolus lunatus L.), cowpea (Vigna sinensis Endl.), runner bean (Phaseolus coccineus L.), and peanut (Arachis hypogaea L.) were then tried.

Selected plant hosts for life history determinations had to be grown under protection from violent weather conditions and away from insects other than the species under study. A large screenhouse 30 m long, 10 m wide, and 15 m at the highest point of the slanted roof was built (Fig. 9). All four sides were covered with saran screen and the top was of polyethylene film 0.3 mm thick. The structure was partitioned crossways into two equal sections, one to be used for the

production of plant material free from all insect contamination and the other to rear test insects. It was oriented in a general east-west direction for protection against the often violent rains and winds originating from the northeast. The floor was of coarse ground volcanic rock for rapid drainage.

The plants were grown in long wooden boxes, 9 m long, 60 cm wide, 45 cm high, the bottoms of which were perforated and garnished with a 5-mm layer of pebbles. All soil used in growing plants was fertilized with a nitrogen-rich formula of the type 20-10-10.

The wooden boxes were set on benches to ease observation and handling (Fig. 11). The insects were reared in cages 60 cm long, 60 cm wide, and 50 cm high (Fig. 13). The two lateral sides and the back were covered with saran screening. The upper half of the front was lined with plexiglass and the lower half was occupied by a sleeve of light cotton cloth. To feed the colonies of leafhoppers, selected bean species were grown in wooden flats 50 cm x 40 cm x 15 cm which could be introduced within the cages through the sleeve.

Records were kept of the temperature and moisture within the screenhouse with the help of a recording hygrothermograph. Typical readings for a complete year are listed in Table 2. Because the screenhouse was fairly tall, the hot air accumulated at a height which could not adversely affect either plants or insects. Even during the lull marking the daily breeze shift from the northeast to the southwest, no harmful effect was ever recorded. In fact, up to a height of about 5 meters,

Table 2. Screenhouse humidity and temperature recordings at Turrialba, Costa Rica, for the period July 1966-June 1967

Week	Humidity		Temperature	
	Maximum	Minimum	Maximum	Minimum
July 4-11, 1966	93%	48%	30°C	18°C
11-18, 1966	93%	48%	32°C	19°C
18-25, 1966	94%	49%	31°C	18°C
25-Aug. 1, 1966	94%	52%	31°C	18°C
AVERAGES FOR JULY 1966	93.5%	49.3%	31°C	18.3°C
Aug. 1-8, 1966	95%	47%	31°C	17°C
8-15, 1966	95%	44%	31°C	19°C
15-22, 1966	94%	44%	33°C	19°C
22-29, 1966	95%	47%	31°C	17°C
29-Sept. 5, 1966	94%	48%	31°C	19°C
AVERAGES FOR AUGUST 1966	94.4%	46.0%	31.4°C	18.2°C
Sept. 5-12, 1966	95%	43%	32°C	18°C
12-19, 1966	95%	43%	33°C	17°C
19-26, 1966	94%	42%	32°C	18°C
26-Oct. 3, 1966	95%	40%	31°C	18°C
AVERAGES FOR SEPT. 1966	94.7%	42.0%	32.0°C	17.8°C
Oct. 3-10, 1966	95%	38%	38°C	18°C
10-17, 1966	95%	43%	38°C	19°C
17-24, 1966	96%	40%	39°C	18°C
24-31, 1966	94%	36%	38°C	19°C
31-Nov. 7, 1966	95%	50%	30°C	18°C
AVERAGES FOR OCT. 1966	95.0%	41.4%	36.6°C	18.4°C
Nov. 7-14, 1966	95%	44%	30°C	15°C
14-21, 1966	95%	44%	31°C	15°C
21-28, 1966	95%	50%	30°C	17°C
28-Dec. 5, 1966	96%	41%	30°C	16°C
AVERAGES FOR NOV. 1966	95.3%	44.8%	30.3°C	15.8°C

Table 2. (continued)

Week		Humidity Maximum	Humidity Minimum	Temperature Maximum	Temperature Minimum
Dec.	5-12, 1966	95%	53%	30°C	17°C
	12-19, 1966	91%	45%	29°C	17°C
	19-26, 1966	94%	44%	30°C	16°C
	26-Jan. 2, 1967	95%	44%	38°C	18°C
AVERAGES FOR DEC. 1966		93.8%	46.5%	31.8°C	15.8°C
Jan.	2-9, 1967	96%	34%	34°C	15°C
	9-16, 1967	97%	45%	34°C	17°C
	16-23, 1967	94%	40%	35°C	16°C
	23-30, 1967	95%	44%	38°C	16°C
	30-Feb. 6, 1967	97%	40%	38°C	14°C
AVERAGES FOR JAN. 1967		95.8%	40.6%	35.8°C	15.6°C
Feb.	6-13, 1967	96%	35%	37°C	15°C
	13-16, 1967	95%	40%	36°C	16°C
	22-27, 1967	96%	38%	35°C	15°C
AVERAGES FOR FEB. 1967		95.7%	37.7%	36.0°C	15.3°C
Mar.	1-6, 1967	94%	28%	36°C	14°C
	5-13, 1967	96%	33%	35°C	16°C
	14-20, 1967	97%	30%	35°C	14°C
	20-27, 1967	98%	30%	37°C	14°C
	27-Apr. 3, 1967	97%	32%	36°C	15°C
AVERAGES FOR MAR. 1967		96.4%	30.6%	35.8°C	14.6°C
Apr.	3-10, 1967	95%	38%	32°C	18°C
	10-17, 1967	97%	43%	36°C	18°C
	17-24, 1967	96%	42%	37°C	18°C
	- -	-	-	-	-
AVERAGES FOR APR. 1967		96.0%	41.0%	35.0°C	18.0°C

Table 2. (continued)

Week		Humidity Maximum	Humidity Minimum	Temperature Maximum	Temperature Minimum
May	1-7, 1967	97%	36%	37°C	16°C
	8-15, 1967	96%	42%	37°C	19°C
	15-22, 1967	97%	39%	37°C	17°C
	22-29, 1967	97%	42%	37°C	19°C
	29-June 5, 1967	97%	44%	36°C	18°C
AVERAGES FOR MAY 1967		96.7%	39.8%	36.8°C	17.8°C
June	5-12, 1967	96%	37%	36°C	18°C
	12-19, 1967	97%	40%	38°C	19°C
	- -	-	-	-	-
	28-July 4, 1967	95%	44%	38°C	18°C
AVERAGES FOR JUNE 1967		96.3%	41.3%	37.3°C	18.3°C

the temperature inside and outside the screenhouse differed by only 1 or 2 degrees. The roof and the sides did modify normal radiation, however, with the result that the plants were abnormally elongated, although they did not appear chlorotic or adversely affected in any other way.

Building and plant boxes were kept regularly sprayed with Tedion to prevent establishment of phytophagous mites. The colonies of leafhoppers were often invaded by hordes of a small black-headed ant, Tapinoma melanocephalum Fab., which readily devoured the small nymphs. The benches supporting the cages had to be kept sprayed with a persistent insecticide, most commonly Aldrin. At one time, anthracnosis (Colletotrichum lindemuthianum Sacc. and Magn.) became a serious problem on our common bean plantings (Phaseolus vulgaris L.) but was successfully eradicated thereafter by fumigation of the soil with methyl bromide prior to filling the troughs. In addition, to prevent the buildup of any pathogen, the soil at the end of each growing cycle was replaced with a freshly fumigated lot and the containers scraped and washed. Minor outbursts of angular leaf spot and powdery mildew could be controlled before they got out of hand.

Under field conditions it could easily be observed that certain cultivars of common bean were especially suitable host plants. In the interest of including a range of commercially grown legumes in the life history studies, legumes that are fast growing, of small growth habit, and readily accepted by leafhoppers were sought. The following

were selected:

Kidney bean: Phaseolus vulgaris L. var. S-19-N

Lima bean : Phaseolus lunatus var. Henderson baby lima

Cowpea : Vigna sinensis

From a variety trial of some 300 entries in Honduras the kidney bean cultivar, S-19-N, well met the criteria above. In addition, it grew erect, was tolerant of diseases, and, except in mild attacks of powdery mildew, grew well and produced great amounts of foliage.

A sample lot of Henderson baby lima bean was obtained from the United States Department of Agriculture at Beltsville, Maryland. The variety proved suitable and large quantities of seeds could be purchased from commercial houses. Seeds of cowpea of a suitable, but unfortunately unidentified variety were available at the Turrialba Center in ample amounts.

Selection of Oviposition Site

Since the eggs of E. phaseola are inserted into the plant where they are scarcely visible, it was necessary to discover which plant regions were used in oviposition. With this information it would be possible to develop appropriate techniques for collecting and observing the development of the egg stage.

The cowpea and lima bean were used in this test. Suspecting that the oviposition might vary with the stage of development of the plant host, potted seedlings, respectively 12, 15 and 24 days old, were used and 3 replicate plants were provided in each age group. Essentially, at 12 days the young plant has only its simple leaves but these are

fully developed. The 15-day plant has its first trifoliate leaf and a terminal shoot with rudimentary compound leaves. At 24 days of age, the plant has developed 4 trifoliate leaves; the terminal shoot is now a stringy leader with possibly one additional leaf bud; the simple leaves are still present and have not dropped.

The plants were caged from the time the seeds were sown. The cages were simple cylinders of inert plastic sheeting of such a diameter that they could be inserted into the soil of earthen pots 30 cm in diameter. The upper end of the cage was closed with fine nylon gauze held in place by a rubber band. When the plant had reached the desired age, female leafhoppers known to be ovipositing were introduced through a round opening in the side of the cylinder at the rate of 2 insects per fully spread leaf and 1 additional for the terminal growth.

The caged plants were set up in a laboratory that measured about 8 m x 10 m and had two wide bay-windows opening to the north. Temperature was maintained fairly constant at about 25°C and the relative humidity fluctuated between 50 and 70%. Four 2-tube, 24-ft fluorescent ceiling lamps provided abundant illumination.

The plants were observed for 3 days from 5:00 a.m. to 6:00 p.m. and at irregular intervals during the evening up to 11:00 p.m. The insects seemed to spend the major part of their time on the underside of leaves but were also seen for variable periods on the leaf petioles and on the stem. They were not observed to be particularly attracted to the succulent terminal shoots and showed preference for the trifoliate leaves only if these were fully expanded. Following exposure to the

insects, the plants were cut into sections and cleared in hot lactophenol according to the method perfected by O. V. Carlson and E. T. Hibbs (1962). The eggs were counted and averaged for each plant section. A similar procedure was used for lima bean, but only of one age, namely 15 days. The results are represented graphically in Fig. 24 and summarized below in Table 3.

Table 3. Number of eggs per section of cowpea (Vigna sinensis) and lima bean (Phaseolus lunatus)

Plant sections	Cowpea			Lima bean
	12 days	15 days	24 days	15 days
1. Stem below simple leaves	1	0	0	0
2. Petioles of simple leaves	22	9	4	4
3. First internode	31	3	0	0
4. Petiole of first trifoliate	-	31	20	4
5. Second internode	-	6	0	0
6. Petiole of second trifoliate	-	3	21	9
7. Median leaflet of first trifoliate	-	-	-	6
8. Third internode	-	-	0	-
9. Petiole of third trifoliate	-	-	38	-
10. Fourth internode	-	-	0	-
11. Petiole of fourth trifoliate	-	-	3	-
12. Terminal growth	-	-	29	-

In summary:

1. The placement of eggs is shifted in an upward direction as the plant grows and matures.
2. No eggs were found within leaf veins of cowpea or lima bean.
3. Youthful (terminal) growth is not sought after for egg deposition.

4. Leaf petioles are a choice site, regardless of leaf age, except for the very early or very late stages of leaf development.
5. The terminal growth becomes a significant oviposition site late in the development of the foliage after the lower parts of the plant have aged.

In lima bean, the leaflets are attached by petiolules to a common petiole or rachis. This feature was expected to inform further on the localized character of the oviposition site. Indeed, the eggs were observed clustered in the central petiolule.

The favorite oviposition site was thus determined and subsequent observations could be made about the development cycle of E. phaseola. The snapbox technique perfected by O'Keeffe (1965) was used extensively.

Rate and Duration of Oviposition

The total number of eggs laid by mated females was determined by maintaining the insects on excised petioles within 3.5 x 3.5 x 3.5 cm clear polystyrene plastic boxes. A lateral aperture 0.8 cm in diam. was provided for the introduction of the test insect. The plant material was renewed every 2½ to 3 days and the cages cleaned of honeydew. Eggs were counted in petioles cleared in hot lactophenol at each period of petiole change until the female died. The time lapse between consecutive petiole changes was precisely recorded so that the oviposition rate per 24 hours could be calculated.

In order to determine whether the type of food might have an influence on either the total number of eggs deposited or the duration of

egg deposition, the three leguminous host plants were sequentially used with approximately 60 specimens in each case. No special consideration was given to the stage of maturity of the plant material. Only mated females were included. Some mated females would not oviposit and were discarded. The data recorded in this exploratory trial are condensed in Table 4.

Table 4. Average total number of eggs per female and duration of oviposition of E. phaseola on three leguminous hosts

	Phaseolus vulgaris	Phaseolus lunatus	Vigna sinensis
Total eggs laid per female	159.23	115.97	32.43
Duration of oviposition (days)	74.97	64.97	61.12

Egg development

Plants with fertilized eggs in their tissues were removed from the oviposition cages and the presence of females to controlled conditions of a growth chamber. The plants were examined at frequent intervals especially in the morning. The date and hour of emergence were noted and the first instar nymphs were removed with a fine camel's-hair brush (wetted in distilled water) as soon as they would emerge and start toward the neighboring leaf. The average incubation period was between 8 and 10 days.

Oviposition by Virgin Females

All excised petioles from all cages were processed at each change and searched for eggs. This led to the finding that some females which had not been observed copulating were, nevertheless, depositing eggs.

In order to establish whether or not virgin females deposited viable eggs, fifth instar nymphs were collected from one of the leafhopper colonies on common bean and introduced individually into cages with bean petioles. At emergence, the males were discarded and the females maintained encaged through 4 changes of petioles, (i.e. about 12 days). The petioles at each change were cleared in lactophenol and examined for eggs. The numbers of eggs which were counted from 20 such virgin females are tabulated in Table 5. These ovipositing, non-mated females were then placed on potted young bean plants which were free of infestation. They were allowed to stay 6 days and were then liberated. The plants, now without cages, were introduced in controlled environment chambers and observed for emergence of nymphs (Fig. 16).

After 7 days, and later after 10 days, 3 plants were selected at random, and the sections processed in lactophenol and searched for developing eggs. The eggs from the virgin females showed no definite outline or content; instead, oblong cavities, slightly tan-colored, were observed suggesting the emplacement of eggs which had failed to develop and had decayed.

Table 5. Oviposition by virgin females

Female number	Periods during which eggs were counted (3 days)			
	1	2	3	4
1	0	0	0	6
2	0	0	0	0
3	0	0	7	7
4	2	7	-[a]	-[a]
5	5	7	-[a]	-[a]
6	0	5	-[a]	-[a]
7	7	9	-[a]	-[a]
8	0	0	8	4
9	0	0	3	9
10	0	0	8	4
11	0	5	0	0
12	0	0	4	1
13	6	11	0	0
14	0	0	3	6
15	0	0	0	0
16	0	0	6	0
17	0	0	9	6
18	0	0	7	3
19	0	0	0	0

[a]Egg count omitted by error.

Nymphal Development

All nymphs born in the course of one day were promptly transferred to rearing cages 3.5 x 3.5 x 3.5 cm hinged plastic boxes attached by way of rubber tubing to florist's waterpicks filled with 3% sucrose solution. Petioles with petiolules and a small section of leaf area were used as food substrate. The portion of foliar surface was intended to facilitate the feeding of newly born nymphs and offer them a shaded site, since at that stage of their development leafhoppers display strong negative phototropism.

All cages were numbered and examined twice daily at 6:00 a.m. and 6:00 p.m. The duration of the different instars was determined by the number of exuviae. The shed skins were counted at each observation and each additional one meant the passage from one instar to the next (up to a maximum of 4), at which time the adult emerged. The days were divided into two halves of 12 hours each; the moultings (if any) occurring during the night or early morning falling into the first half and those occurring during the day into the second half. The time of emergence of the adult was recorded and the sex determined.

All three legumes were tried as food substrates mostly to determine whether they would present any problems and could be safely included in planned experiments. Table 6 summarizes the data which were thus obtained and they are expressed both as individual instars and total average length of the development cycle. The given data represent averages over 38, 42, and 31 specimens raised respectively for at least 10 consecutive generations on common bean, lima bean, and cowpea.

Table 6. Average duration (in days) of the nymphal stage of E. phaseola reared on three leguminous hosts

Host plants	Instars I	II	III	IV	V	Total duration
Phaseolus vulgaris	2.20	1.87	1.97	2.04	3.61	11.66
Phaseolus lunatus	2.51	1.84	2.04	2.39	3.85	12.60
Vigna sinensis	3.31	2.13	2.37	2.53	3.84	14.19
Means	2.67	1.95	2.13	2.32	3.77	12.84

Sex Ratio

Among the 111 individuals which successfully completed their development on the three leguminous hosts, the sexes were found to be distributed as follows:

Table 7. Sex ratio of E. phaseola reared on three leguminous hosts

Plant host	Females	Males	Totals	Male:Female sex ratio
Phaseolus vulgaris	18	20	38	1.07
Phaseolus lunatus	20	22	42	1.10
Vigna sinensis	15	16	31	1.12
TOTALS	53	58	111	1.09

The overall sex ratio was thus found to be 1.09, indicating a very slight predominance of male births.

Longevity of Mated Females

The life-span of inseminated females of E. phaseola was evaluated on all three substrate types. The observation cages attached to water-picks in the usual manner were of slightly larger dimensions, 4.5 x 5.5 x 3.5 cm, to accommodate a longer section of petiole and median petiolule. The food was renewed at suitable intervals and the snapboxes freed of honeydew. This cleaning was found to be increasingly important as the specimens aged and weakened. They would frequently be observed with the wings glued to the sugary exudate, trying to free themselves. The specimens found dead, immobilized by honeydew, were discarded from the computations. Table 8 summarizes longevity figures averaged on 37 mated females reared on common bean, 38 on lima bean, and 34 on cowpea.

Table 8. Longevity of mated females of E. phaseola on three leguminous hosts

Host plants	Average number of days lived
Phaseolus vulgaris	76.78
Phaseolus lunatus	62.89
Vigna sinensis	61.82
Overall mean longevity	67.16

Mating

Another adaptation of O'Keeffe's technique was used in that test. It consisted essentially in maintaining appropriate sections of plant

material in a fresh condition within small observation cages of clear plastic. Leaf petioles were used with the central petiolule attached. The sections measured totally about 8 cm and the cut end was immersed in a 3% sucrose solution contained in a florist's waterpick. The observation cage was a plastic snapbox, 4.5 x 5.5 x 3.5 cm, clasped on a piece of plastic tubing 0.9 cm in diameter, about 4 cm long, thrust into the neoprene cap of the waterpick. The snapbox was provided at the side with an additional circular hole for the introduction of test insects.

After it was found that several test insects would be killed accidentally while snapping the cage closed, a small modification was introduced, as seen in Fig. 17. Instead of having the snapbox clasped to the tubing thrust into the waterpick, the piece of tubing was made to fit tightly into a round opening provided on one half of the snapbox. The latter could be opened within a transfer cage (Fig. 23), cleaned of honeydew, or otherwise manipulated without separating cage and waterpick. The insect naturally escaped but was retrieved easily with a small glass tube and returned to the cage now clean. Cleaning of the observation cages and renewal of the plant material were performed together. The transfer cage was 60 cm long, 50 cm wide, 50 cm tall, with sides of fine saran screening and a top of plastic film. The front part was divided into two halves; the upper, fitted with plexiglass, served as an observation window; the lower was furnished with black cloth to be used as a sleeve.

To facilitate recapture, a bright light source was sometimes

maintained opposite the transparent top. When eggs had to be counted, the petioles, before clearing in hot lactophenol, were identified with labels of bond paper strung with No. 10 gauge sewing thread.

In the course of the research, mating pairs were often observed in the screenhouse and in the laboratory. It became promptly evident that copulation was more frequent in the early morning hours. Some matings did occur late in the forenoon; very few were observed in the afternoon and none in the evening. To determine whether copulation would occur during the night, visits were occasionally made to the laboratory, though not as regularly and frequently as during the daytime. The lights were not switched on and inspection was carried out with a flashlight. The insects were found to be extremely quiet and inactive in contradistinction to the great mobility and restlessness which are displayed when matings are frequent.

The mating schedule as mentioned above was not disrupted under conditions of controlled temperature and humidity nor under artificial illumination. The intensity of light did not seem to have any significant effect, as evidenced by comparable activity during bright and cloudy days. Although day lengths in the Tropics do not vary appreciably at different times of the year, slight variations do occur and photoperiod in the laboratory was changed to mimic the field conditions. In general terms, an average day is equally divided between daylight and darkness.

A first group of 52 females was observed on common bean (Phaseolus vulgaris L.). About 200 fifth instar nymphs were collected from the

rearing cages in the screenhouse and introduced individually in observation cages, 3.5 x 3.5 x 3.5 cm, with bean petioles as food. Records were kept of the time of emergence of both sexes and of the time that males were introduced into the cages of the virgin females, which were numbered. Two males were provided for each female.

Observations were made at hourly intervals from about 5:30 a.m. to 6:00 p.m. The time and duration of copula were recorded. They are summarized in Tables 9, 10 and 11. Once mating was accomplished, the males were promptly removed and the inseminated females were retained encaged, under the same identifying number, for study of oviposition and longevity. As mentioned earlier, the food was renewed about every 3 days, at which time the cage was cleaned of honeydew with a swab of cotton dipped in distilled water.

Although no particularly long time was spent watching mating behavior, many of the events reported by workers such as O. V. Carlson (1967) were noted, e.g. increase in activity, preening, parallel positioning of the mates, swift circling ending in the interlocking of the genital appendages, tapping of the sides of the male by the female while in copulo. Interlocked male and female reacted in unison to brisk disturbances in the environment such as shift in the substrate, sudden change in illumination, strong noises, and movements of surrounding persons or objects. The mating couple would move in harmonious coordination and, as a rule, would not separate, except perhaps, if they had been copulating for considerable time. Pairs accidentally shaken off foliage dropped onto the bottom of the cage or onto the soil and

Table 9. Time and duration of mating of *E. phaseola* on common bean (*Phaseolus vulgaris*)

Beginning observed at:	Termination observed at:	Total duration (hours)
7:30 a.m.	9:00 a.m.	1 hr 30 min
7:10 "	10:15 "	3 " 05 "
6:35 "	8:00 "	1 " 25 "
6:30 "	7:40 "	1 " 10 "
12:45 p.m.	2:15 "	1 " 30 "
6:35 a.m.	9:00 "	2 " 25 "
4:30 p.m.	6:30 p.m.	2 " 00 "
7:45 a.m.	9:45 a.m.	2 " 00 "
6:00 "	8:40 "	2 " 40 "
5:45 "	8:15 "	2 " 30 "
9:20 "	10:00 "	0 " 40 "
5:45 "	7:40 "	1 " 55 "
6:00 "	8:50 "	2 " 50 "
5:45 "	8:20 "	2 " 35 "
8:30 "	10:30 "	2 " 00 "
5:30 "	7:30 "	2 " 00 "
6:30 "	8:00 "	1 " 30 "
6:00 "	8:00 "	2 " 00 "
7:00 "	9:10 "	2 " 10 "
6:00 "	7:45 "	1 " 45 "
8:00 "	10:15 "	2 " 15 "
6:30 "	8:20 "	1 " 50 "
8:10 "	10:30 "	2 " 20 "
7:15 "	9:30 "	2 " 15 "
6:00 "	7:45 "	1 " 45 "
6:00 "	8:30 "	2 " 30 "
9:30 "	10:50 "	1 " 20 "
6:30 "	8:10 "	1 " 40 "
6:00 "	8:30 "	2 " 30 "
8:15 "	10:30 "	2 " 15 "
6:00 "	8:40 "	2 " 40 "
6:00 "	7:25 "	1 " 25 "
10:30 "	12:05 p.m.	1 " 35 "
6:30 "	8:10 a.m.	1 " 40 "
5:45 "	7:30 "	1 " 45 "
7:40 "	8:00 "	0 " 20 "
6:00 "	8:40 "	2 " 40 "
	Total time	66 " 05 "
	Number of pairs. . . .	37
	Mean mating duration .	2 hr 20 min

Table 10. Time and duration of mating of E. phaseola on lima bean (Phaseolus lunatus)

Beginning observed at:	Termination observed at:	Total duration (hours)
6:30 a.m.	9:00 a.m.	2 hr 30 min
5:10 "	7:20 "	2 " 10 "
5:25 "	7:45 "	2 " 20 "
6:00 "	8:00 "	2 " 00 "
5:35 "	6:45 "	1 " 10 "
5:20 "	7:45 "	2 " 25 "
5:30 "	7:45 "	2 " 15 "
5:30 "	6:40 "	1 " 10 "
7:00 " [a]	9:00 "	2 " 00 "[a]
6:15 "	7:20 "	1 " 05 "
9:30 "	10:40 "	1 " 10 "
5:30 "	8:00 "	2 " 30 "
6:00 "	7:40 "	1 " 40 "
7:15 "	8:15 "	1 " 00 "
7:00 "	8:30 "	1 " 30 "
6:00 "	8:40 "	2 " 40 "
5:45 "	8:00 "	2 " 15 "
7:30 "	8:50 "	1 " 20 "
5:30 "	7:30 "	2 " 00 "
5:15 "	7:30 "	2 " 15 "
3:40 p.m.	4:45 p.m.	1 " 05 "
9:00 a.m.	11:00 a.m.	2 " 00 "
7:20 "	8:35 "	1 " 15 "
5:15 "	8:00 "	2 " 45 "
5:20 "	8:00 "	2 " 40 "
5:45 "	7:15 "	1 " 30 "
10:45 "	12:45 p.m.	2 " 00 "
5:15 "	6:45 a.m.	1 " 30 "
9:45 "	11:00 "	1 " 15 "
5:15 "	7:15 "	2 " 00 "
5:20 "	7:00 "	1 " 40 "
7:00 "	8:30 "	1 " 30 "
8:00 "	9:25 "	1 " 25 "
5:15 "	7:30 "	2 " 15 "
1:30 p.m.	2:30 p.m.	1 " 00 "
6:00 a.m.	7:45 a.m.	1 " 45 "
7:00 "	8:30 "	1 " 30 "
1:00 p.m.	2:30 p.m.	1 " 30 "

[a] Suspected to have started earlier.

Table 10. (continued)

Beginning observed at:	Termination observed at:	Total duration (hours)
5:30 a.m.	6:30 a.m.	1 hr 00 min
7:00 "	8:30 "	1 " 30 "
6:00 "	7:30 "	1 " 30 "
6:45 "	8:50 "	2 " 05 "
5:30 "	7:30 "	2 " 00 "
	Total time	71 " 35 "
	Number of pairs. . . .	43
	Mean mating duration .	2 hr 05 min

Table 11. Time and duration of mating of E. phaseola on cow pea (Vigna sinensis)

Beginning observed at:	Termination observed at:	Total duration (hours)
7:00 a.m.[a]	9:15 a.m.	2 hr 15 min[a]
9:25 "	12:00 "	2 " 35 "
7:00 " a	9:45 "	2 " 45 " a
10:00 "	11:40 "	1 " 40 "
8:35 "	10:30 "	1 " 55 "
6:10 "	8:00 "	1 " 50 "
6:15 "	8:00 "	1 " 45 "
7:00 " a	8:25 "	1 " 25 " a
7:10 " a	9:45 "	2 " 35 " a
9:20 "	11:15 "	1 " 55 "
8:30 "	10:35 "	2 " 05 "
7:30 "	10:45 "	3 " 15 "
6:00 "	8:50 "	2 " 50 "
7:20 " a	10:40 "	3 " 20 " a
7:00 " a	8:30 "	1 " 30 " a
7:00 " a	9:15 "	2 " 15 " a
6:20 " a	7:50 "	1 " 30 " a
7:30 "	11:45 "	4 " 15 "
6:15 "	8:00 "	1 " 45 "
8:30 "	11:15 "	2 " 45 "
7:50 "	9:15 "	1 " 25 "
7:00 " a	9:35 "	2 " 35 " a
7:10 "	11:10 "	4 " 00 "
9:50 "	12:30 "	2 " 40 "
6:35 "	8:00 "	1 " 25 "
8:50 "	10:30 "	1 " 40 "
7:00 " a	10:30 "	3 " 30 " a
7:00 " a	10:00 "	3 " 00 " a
8:30 "	11:30 "	3 " 00 "
7:00 "	9:00 "	2 " 00 "
7:00 " a	9:00 "	2 " 00 " a
	Total time	67 " 05 "
	Number of pairs. . . .	31
	Mean mating duration .	2 hr 16 min

[a]Suspected to have started earlier.

remained coupled. In general, however, all possible causes of disturbance were carefully avoided, especially at the times when matings were at a peak, between 5:00 a.m. and 11:00 a.m.

In addition to information about time and duration of mating, the ages of both sexes at mating were also recorded and are summarized in Table 12. In order to bring out such information as length of premating in either sex, relative importance of male and female ages in determination of mating, interaction of male and female ages, the mating data were organized as follows:

a. Age of female at exposure to males
b. Age of males at exposure to female
c. Time lapse between exposure of sexes to each other and mating occurrence
d. Age of female at mating
e. Age of the males at mating (it was not difficult to use males of the same age, that is, born the same day).

A statistical analysis was made of these data and is presented within the experimentation section.

Feeding of Empoasca leafhoppers on Legumes

The great majority of bean fields in Central America are invariably invaded by Empoasca leafhoppers. Many wild species appear also to be particularly sought after by the insects. Generally, two to three bean plantings are realized in one year. The first is initiated as soon as the "spring" rains have started in April and is harvested by late June to mid-July,

Table 12. Mating age (in days) of *E. phaseola* on *Phaseolus vulgaris*

Age of female at exposure to males	Age of males at exposure to female	Time lapse between exposure and mating	Age of female at mating	Age of males at mating
2	0	7	9	7
0	0	12	12	12
0	0	7	7	7
5	0	6	11	6
6	35	12	18	47
0	0	6	6	6
1	1	3	4	4
5	6	3	8	9
0	14	6	6	20
6	0	3	9	3
2	9	4	6	13
5	7	1	6	8
3	21	7	10	28
6	0	5	11	5
3	0	5	8	5
2	0	2	4	2
4	5	2	6	7
2	0	7	9	7
1	1	8	9	9
1	1	8	9	9
6	1	5	11	6
1	1	9	10	10
6	0	6	12	6
0	11	5	5	16
1	21	10	11	31
8	0	4	12	4
2	0	7	9	7
2	0	5	7	5
2	5	12	14	17
9	7	0	9	7
2	4	4	6	8
4	8	2	6	10
0	10	27	27	37
0	8	12	12	20
0	0	9	9	9

in dry weather. The second is established in early August and is mature in November, when the second rainy season is over. Empoascan leafhoppers build up during the first crop and transfer in great numbers to the second, jeopardizing or annihilating all production of commercial beans. Most often, the plantations will not fail altogether but will be diversely affected, depending on the intensity of the invading population. When the pest density is very high, the bean field will quickly be damaged beyond recovery and the leafhoppers will disperse to other food plants.

An infestation of moderate intensity will detain apical growth and bring about a profusion of axillary branching which largely compensates for the arrested terminal elongation. If the infestation persists, stunting of new growth, crinkling and roughening of the foliage will develop. After some time, the foliage will start to yellow. In the sequence of symptoms, yellowing is really the one which raises alarm in the farmer. Strangely, the other damage expressions, though of greater physiological consequence, often escape notice or are not associated with the presence of the insects. In the areas where E. phaseola predominated, damage expression was less striking, though essentially the same as for kraemeri, and was given even lesser consideration.

The plant reaction to leafhopper attack was observed to vary in different types of legumes. Common bean (Phaseolus vulgaris L.) showed great sensitivity to the insect attack, reacted with abundant axillary growth, encouraging further proliferation of the pest, and succumbed

rapidly to its damage. In the screenhouse, the cages had to be infested with relatively few insects so that the abundant progeny would find food enough to complete its development. Lima bean (Phaseolus lunatus) fostered numerical increase to a much lesser extent. If the invading population is strong, it will seldom succeed in killing the plants; instead, that population will dwindle and will sometimes come close to extinction. The plants are heavily damaged but will recuperate, producing new foliage for the progeny and the few survivors (Fig. 10). Cowpea (Vigna sinensis) will tolerate high numbers of insects without apparent damage; axillary compensation is slow and of little significance. Under field conditions, nymphs are seldom seen on the latter species, indicating that it is not readily infested.

The pattern, as well as the extent of yellowing, were observed to be different with the two predominant species of Cicadellidae (Figs. 18 and 19). E. kraemeri damage, in addition to developing faster, showed a pattern which recalls hopperburn; i.e. a marginal drying up of the tissues, downward (instead of upward) curling of the foliar edge. E. phaseola damage is slower to develop and displays a distinct angular yellowing. In contrast to the damage inflicted by E. kraemeri (Fig. 19, lower series of 3 leaves), the damage by E. phaseola may never extend to the entire marginal area of the leaf (Fig. 19, upper 3 leaves) unless necrosis sets in, completely destroying the leaf (Fig. 18, upper left corner). Fig. 18 shows in a clockwise order, the progressive changes which took place in the bean leaf as a result of damage by E. phaseola, the healthy leaf occupying the center of the illustration.

From the preceding observations and exploratory trials it was obvious that the feeding and oviposition of E. phaseola were far from being indiscriminate and that the quality and type of the substrate had to be taken into account if the biological processes of the leafhopper were to be assessed with some degree of precision.

The observations and trials carried out indicated plainly that E. phaseola displays different rates of oviposition and longevity on different host plants. One plant species will foster the reproduction and lengthen the life of the insect and others will prove to be less favorable substrates. None of the three legumes included in the tests interfered drastically enough with the biology of the leafhopper to suggest potent inhibitory qualities, though inhibitors may occur in other strains. It has already been mentioned that the observed lack of attractiveness of cowpea to leafhoppers in the field is overcome in confinement. It would be of great interest to determine what plant quality is the basis for the insects limited acceptance.

EXPERIMENTATION

Two experiments were conducted to measure the influence of the host plant upon fecundity and longevity of E. phaseola.

Experiment I

The object of this experiment was to measure and compare the rate of egg deposition and its duration among females restricted to common bean plants of pre-bloom and post-bloom maturity and to observe whether or not the oviposition rate would be influenced (and how quickly influenced) if ovipositing females were transferred after 30 days on petioles of post-bloom plants to the petioles of pre-bloom plants.

Materials and methods

Greenhouse plantings of common bean were timed to provide abundant plants of pre-bloom and post-bloom maturity during the course of the experiment. (Figs. 14 and 15).

Erlenmeyer flasks (500 cc), filled with 3% sucrose solution, were fitted with cork stoppers in which 4 holes were perforated. Four leaves clipped from the median portion of mature plants, about 30 days from planting, were cautiously introduced through the holes in the stoppers and the cut ends of the petioles immersed in the sugar solution (Fig. 20). The leaf blades were oriented as far apart as possible to avoid overshadowing and to provide aeration and freedom of movement for the insects engaged in feeding and mating. The flasks were scattered over the available bottom surface of a transfer cage (Fig. 12) which was lighted with a 2-tube fluorescent lamp set close to the transparent plastic top.

The test insects were taken from several rearing cages in which leafhoppers had been continuously raised on the same host for at least 8 to 10 generations. They were captured as fifth instar nymphs and taken to the laboratory, where about 500 of the nymphs were released gently and uniformly over the foliage in a transfer cage. Here they were held for 9 days, 2 for the completion of the last instar and 7 for premating. The cage was frequently observed for emergence to the adult form and possible mating. Pairs in copula started to show in appreciable number around the 7th day and continued through the 8th and 9th. Early on this last day the sexes were separated and the females individually caged.

Groups of 50 individually caged females were distributed randomly among the following treatments:

A. Oviposition cage continuously supplied with petioles of plants in pre-bloom stage

B. Oviposition cage supplied with petioles of post-bloom plants for 30 days, then transferred to pre-bloom petioles

C. Oviposition cage continuously supplied with post-bloom petioles.

The oviposition cages were clear plastic snapboxes 3.5 x 3.5 x 3.5 cm with three holes, one slightly larger than an average petiole (about 4 mm in diam), a second on the opposite side wide enough to receive a piece of plastic tubing 7 mm in diam, and a last one on the lateral side of the hinged half of the snapbox, about 5 mm in diam.

The excised leaf was inserted first through the small upper hole, then cautiously pushed across the section of tubing, the free end immersed in a florist's waterpick filled with a 3% sucrose solution (Fig. 22). Before the cages were closed, cotton was gently caulked around the petiole at the apertures to prevent escape of the female and protect the plant part against rupture or bruises. It was soon seen preferable to first wrap the petioles in wetted cotton prior to their insertion in the snapboxes at a height corresponding to the upper hole, perfecting the caulking later with a pointed instrument. It was easier and less hazardous to install the cotton plug around the base of the petiole in the section of plastic tubing. The cages were then ready to receive the females which were introduced through the lateral hole, which was closed with a cotton plug.

Leaves from the sequential plantings in the greenhouse were collected to supply the oviposition cages in the following manner. Approximately 160 leaves, from pre-bloom plants (27 days from planting), or from post-bloom plants (39 days from planting), were clipped close to their junction with the stem, placed to stand in water, and promptly taken to a cool and well illuminated room. To accomplish this with the least damage to the plant material, shallow enamel pans were used. Rectangular sections of 4-in. mesh hardware cloth were cut and mounted on wooden frames to fit into the pans and to come up flush with the containers brim. The pans were filled with water so that the leaves' petioles would be immersed while the blades rested flat on the screen surface.

At the time of foliage renewal and egg count, the petioles were clipped at the upper surface of the cage, pulled gently 2 to 3 cm out of the plastic tube and again clipped. Pulling out the petiole a short distance was necessary because, often, the insect would oviposit very close to the petiole base or even descend within the tube to deposit eggs. The sections thus excised represented rather exactly the length of substrate on which the female had been feeding and ovipositing. The petioles were slit lengthwise with a razor blade, labelled, and cleared in boiling lactophenol for 2½ minutes. The practice was soon adopted to let them stand in cold lactophenol overnight, the egg count to be carried out the following morning.

Records were kept of the number of eggs deposited and the number of days lived. This made possible the assessment of the following biological variables: (1) number of eggs deposited during the insect's entire life as a fertilized female, (2) duration of the oviposition period, (3) daily oviposition rate, (4) overall rate of oviposition for the total period of egg deposition, and (5) the total life-span.

The daily oviposition rate was determined for each female by dividing the number of eggs deposited in the interval of two consecutive leaf changes by the number of hours that interval lasted and multiplying the quotient by 24. The figures thus obtained were averaged for the number of females alive during the interval being considered.

The curves obtained by plotting the daily oviposition rates against the days of petiole renewal were tempered at first by the relatively large sample size, but became more and more sensitive as the number of surviving females became smaller.

To get away from this bias, an over-all ratio was computed for each individual, dividing the total number of eggs deposited by the total number of days lived. By plotting the values thus obtained, a distribution could be determined, this time on the basis of an over-all level of oviposition (Figs. 26, 27, and 28). Any clustering of points at one age-level would be indicative of the relatively critical importance of this particular period of the insect on fecundity.

Results

Total number of eggs deposited. The effect of treatments A, B, and C on the number of eggs deposited was studied by comparing Treatment A to B, Treatment A to C, and Treatment B to C. For each treatment the mean and the variance were calculated so that t values could be determined for all 3 comparisons mentioned above, as follows:

$$t_{AB} = \frac{\bar{X}_A - \bar{X}_B}{\sqrt{\frac{s_A^2}{n_A} + \frac{s_B^2}{n_B}}} - \frac{176.41 - 153.78}{\sqrt{\frac{15,555.62}{46} + \frac{12,776.06}{46}}} = \frac{22.63}{\sqrt{615.90}} = 0.91$$

$$t_{AC} = \frac{\bar{X}_C - \bar{X}_A}{\sqrt{\frac{s_C^2}{n_C} + \frac{s_A^2}{n_A}}} = \frac{43.39}{\sqrt{544.33}} = 2.12*$$

$$t_{BC} = \frac{\bar{X}_B - \bar{X}_C}{\sqrt{\frac{s_B^2}{n_B} + \frac{s_C^2}{n_C}}} = \frac{26.76}{\sqrt{483.91}} = 1.21.$$

The number of females was 46 in each of the 3 treatments, the number of degrees of freedom per comparison was (46-1) + (46-1) = 90. The corresponding tabulated t values were respectively 1.44 and 2.66 as extrapolated from the values for 60 and 120 d.f.; only comparison AC was significant and only at the 5% level.

Duration of oviposition. The t values calculated for AB, AC and BC were: -0.12, -0.35 and -0.22, respectively. None was significant. In other words, the age of the leaves had no effect on the duration of oviposition in all cases considered.

Daily and overall oviposition rates. These rates are presented in Figs. 25 to 28.

Fig. 25. The lines representing the 3 treatments are all broken, to a greater or lesser extent. No correspondence could be found in the time of occurrence, the frequency or the amplitude of peaks and troughs in the curves. Some features, however, could be observed in all three:

1. An initial steep drop,
2. A gradual return to the original rate level,
3. A steady decrease from the point mentioned under 2 to the termination at zero rate.

A particularly sharp peak at period 17 in the curve describing Treatment A stands out. Time was taken to investigate this apparent abnormality. The individual curves for the females involved in the averaged rate were plotted on the same coordinates and the outstanding peak value was found to represent the correct mean for the values. Reasons for this occurrence will be proposed in the discussion.

Fig. 26 (Treatment A). The majority of the points are located at about a level of 3 and only a few at or near zero. A rather large clumping is present at 120 days. The young plant material would seem to maintain a high oviposition rate throughout the life of the females.

Fig. 27 (Treatment B). The points are scattered and average at about a level of 2.5. There is no clustering at a late age and the duration of oviposition is extended. The number of low values is relatively small. An increase in rate is visible after 30 days, following the transfer from post-bloom to pre-bloom.

Fig. 28 (Treatment C). The rates fall along a line which approximates a level of about 2 and are therefore slightly lower than in the preceding treatments. There can also be observed a greater number of low values between 0 and 1.

Life-span. The longevity means were compared giving the following t values: AB : 1.43, AC : 2.36*, BC : 0.27. Referring again to the tabulated values for 90 d.f. given previously, only AC was significant and only at the 5% level. So, a significant difference in longevity was found only between the females maintained throughout the experiment on either pre-bloom or post-bloom petioles; the change from old to young material showed no significant effect upon longevity.

Experiment II

A second experiment was designed to expose the effect of selected host plants upon the rate and duration of oviposition and as well the longevity of the female leafhoppers. Of the plant species included in

exploratory trials, two legumes, the common bean and the cowpea, were selected. Fecund female leafhoppers raised continuously on each of the two host plants were maintained on the same host or abruptly transferred from one host to the other and the effects noted.

Materials and Methods

Both the common bean and cowpea were easy to grow in the screenhouse and produced foliage in adequate quantity of uniform maturity for implementing the simultaneous treatments.

Plant material of intermediate age (30 days from planting) was used in all cases and the median portions of plants exclusively utilized, avoiding both youthful and decadent foliage. It was assumed that differential levels of physiological activity in the plant, as affected by age, would be minimized if the same degree of plant maturity were provided in all treatments. Petioles and the attached median petiolule, were used in the tests.

These petioles were placed in florist's waterpicks, the lower cut end immersed in 3% sucrose solution. These waterpicks, in turn, were attached (as in Experiment I) by way of a small section of plastic tubing to the feeding and oviposition cages, which were clear plastic snapboxes 5 x 5 x 5 cm. These snapboxes were perforated in the center of the bottom side so that the 0.7 cm hole would be equally divided between the two hinged halves; the second hole was bored on one of the two lateral sides.

Approximately 500 fifth instar leafhopper nymphs were collected from screenhouse colonies which had been maintained successfully for

about 10 generations. Half the number of immature insects were taken from common bean and half from cowpea. The insects from each source were placed in separate breeding cages, where each group was grown to the adult stage and permitted to mate in common.

Individual female leafhoppers were removed from the breeding cages to the appropriate oviposition cages in groups of 50 per test, each oviposition cage containing a leaf petiole of the appropriate test plant to accomplish the following five treatments:

I: Reared on cowpea, tested on cowpea (V → V).

II: Reared on cowpea, tested on common bean (V → P).

III: Reared on common bean, tested on cowpea (P → V).

IV: Reared on common bean, tested on common bean (P → P).

V: Reared on common bean, tested for 30 days on cowpea, returned to common bean, (P → V → P).

The petioles and the sucrose solution were renewed every 2½ to 3 days and the cages cleaned to remove honeydew at each time of change. The plastic oviposition cages were opened within a transfer chamber (Fig. 23) and the petioles gently pulled out of the plastic tubing about 1 to 2 cm. They were then clipped, slit lengthwise to a depth about half their thickness with a razor blade, and labelled. Clearing was carried out in boiling lactophenol for 3 minutes. To avoid mixing, the petioles from each treatment were treated separately and kept immersed in cold lactophenol in labelled beakers.

Records were kept of the number of eggs inserted in the tissues up to the time of death of individual females. These data allowed the

determination, for each treatment, of the following data: (1) number of eggs deposited, (2) duration of oviposition, (3) overall oviposition rate, (4) daily rate of oviposition, and (5) number of days lived.

The analyses presented hereinafter are comparisons of means of 5 samples of unequal sizes but common population variance. The observations are not paired. In order that the statistical treatment be exposed briefly and more clearly, it was thought that symbols could be assigned to the 5 treatments: X_1, X_2, ..., X_5. The means would then be $\bar{X}_1$, $\bar{X}_2$. ...., $\bar{X}_5$; the variances s_1^2, s_2^2,...., s_5^2.

The effect of the rearing host plant, thus, was determined by coupling the means in the following manner: $(\bar{X}_4 - \bar{X}_1) + (\bar{X}_3 - \bar{X}_2)$ or $[(P \rightarrow V) - (V \rightarrow V) + (P \rightarrow P) - (V \rightarrow P)]$, the rearing host plant varies while the experimental host plant does not.

The t value of this effect was calculated, as follows:

$$\frac{(\bar{X}_4 - \bar{X}_1) + (\bar{X}_3 - \bar{X}_2)}{\sqrt{\frac{s_4^2}{n_4} + \frac{s_1^2}{n_1} + \frac{s_3^2}{n_3} + \frac{s_2^2}{n_2}}}$$

The variances were obtained from equations such as shown below for X_1:

$$s_1^2 = \frac{\Sigma X_1^2 - (\Sigma X_1)^2/n_1}{n_1 - 1}$$

The number of degrees of freedom was: $(n_4 - 1) + (n_1 - 1) + (n_3 - 1)$ $(n_2 - 1) = 34 + 49 + 49 + 49 = 181$.

Similarly, the effect of the experimental host plant was determined by a t value calculated as follows:

$$t = \frac{(\bar{X}_2 - \bar{X}_1) + (\bar{X}_4 - \bar{X}_3)}{\sqrt{\frac{s_2^2}{n_2} + \frac{s_1^2}{n_1} + \frac{s_4^2}{n_4} + \frac{s_3^2}{n_3}}}$$; also for 181 d.f.; the

interaction between rearing and experimental host plant, as follows:

$$t = \frac{\bar{X}_1 + \bar{X}_3 - \bar{X}_4 - \bar{X}_2}{\sqrt{\frac{s_1^2}{n_1} + \frac{s_3^2}{n_3} + \frac{s_4^2}{n_4} + \frac{s_2^2}{n_2}}}$$ also for 181 d.f.

A t value was computed separately for comparison IV to V:

$$t = \frac{\bar{X}_5 - \bar{X}_4}{\sqrt{\frac{s_5^2}{n_5} + \frac{s_4^2}{n_4}}}$$. The number of d.f. in that case was: $(n_5 - 1) + (n_4 - 1) = 14 + 34 = 48$.

Results

Total number of eggs deposited. The procedure outlined above was applied at four different ages of the test insects to detect the possible effect of age and also to bring out more strikingly the effect of reverting from the experimental host plant, back to the rearing host plant. The ages chosen were: 15, 45, 75, and 120 days from mating. The calculated t are exposed in Table 13.

Table 13. t values for the effects of rearing and experimental host plant, interaction between the two, and reversion from experimental to rearing host on oviposition of E. phaseola, using common bean (Phaseolus vulgaris) and cowpea (Vigna sinensis)

Variable	Student-t calculated at day			
	15	45	75	120
Rearing host plant	1.48	0.24	0.29	0.26
Experimental host plant	10.09**	15.40**	21.60**	13.59**
Interaction between rearing and experimental host plant	1.17	0.21	0.38	0.19
Reversion from experimental to rearing host plant	0.21	0.12	5.04**	6.31

**Significant at 1% level of probability.

The tabulated values at the 5% and 1% levels for 181 d.f., were, respectively, 2.16 and 2.77. The t values for the rearing host plant failed altogether to show significance, while those of the experimental host plant were very highly significant. The interaction was, in no case, significant and the reversion to the rearing host from the experimental host proved highly significant following the reversion, which was made on the 21st petiole change, i.e. roughly 60 days from mating.

Duration of oviposition. Table 14 summarizes the t values obtained for duration of oviposition in the 5 treatments; the tabulated

values at the 5% and 1% levels are given for 181 (α in the table) and 48 (extrapolated between 45 and 50).

Table 14. Differential effects of rearing and experimental host plants (Phaseolus vulgaris and Vigna sinensis) on duration of oviposition of E. phaseola

Variable	Calculated t values	d.f.	Tabulated t values 5%	1%
Rearing host plant	2.08	181	2.16	2.77
Experimental host plant	9.48**	181	2.16	2.77
Interaction of rearing and experimental host plant	0.83	181	2.16	2.77
Reversion to rearing host plant from experimental host plant	39.62**	48	1.97	2.68

**Significant at the 1% level of probability.

The effects of experimental host plant and of reversion to rearing host were highly significant, while the other effects failed to reach significance.

Daily and overall oviposition rates. The daily rate of oviposition is presented synoptically for Treatments I, II, III, IV, and V in Fig. 29 and the overall rates for these treatments and Treatment V in Figs. 30 to 34.

Fig. 29. All 4 curves have a broken course, occasionally showing a peak of unusual amplitude. The common feature is a gradual downward trend. Depending on the host plant used in rearing, there can be an initial drop (more or less pronounced, e.g. in P → V and P → P), no sharp drop as in V → V, or a rise as in V → P.

Fig. 30 (V → V). The points are clustered from 0 to 40 days and spread thinly from 40 to a little over 145 days. The level of egg deposition is generally low with a maximum of about 4.

Fig. 31 (V → P). The clustering of rather moderately high oviposition rates between 0 and 40 days is not apparent here as in V → V. The overall rate is maintained at 4 or, in some cases, is higher than that rate. Two females oviposited beyond 140 days, although at very low levels.

Fig. 32 (P → P). The points are almost evenly distributed between the relatively high rates of 6 and 2. In all cases the rate was then high, but oviposition was comparatively short as compared to V → V and V → P.

Fig. 33 (P → V). This curve is striking in that all the points are clustered between 0 and a little over 40 days and show a very steep decrease from over 14 down to near 0.

Fig. 34 (P → V → P). The same remarkable pattern is again found as in P → V in the first part of the curve. Oviposition drops to 0 from near 40 to near 80 days and picks up from there, maintaining itself in the vicinity of a 2 overall rate. The duration of the oviposition period is extended beyond 140 days.

Effect of Male and Female Ages on Duration of Premating

A multiple regression analysis made of the male and female mating data in Table 12 resulted in the following analysis of variance:

Table 15. Statistical analysis: Effect of male and female ages on the duration of premating

Source of variation	d.f.	S.S.	M.S.	F
Regression	3			
Female age	1	178.60	178.60	10.05**
Male age	1	52.88	52.88	2.97
Interaction	1	0.35	0.35	0.02
Error	32	568.92	17.77	

**Significant at 1% level of probability.

The F value for the effect of female age is highly significant, the tabulated value at the 1% level being 7.50. The male age and the interaction between the ages of the sexes both failed to show significance even at the 5% level. The tabulated value at that level is 4.15.

DISCUSSION AND CONCLUSION

The results of the experiments and the analysis of their data along with the preliminary observations lead to a few rather well-supported conclusions and also raise several interesting possibilities regarding the relationships of E. phaseola with its host plants in Central America.

On the basis of these studies it may be concluded that:

1. Leguminous plant parts relatively young, but not youthful, are favorably accepted by the leafhopper E. phaseola and have a measurable effect on the number of eggs deposited by that species. If plant material of this quality is fed continuously to females, the duration of the oviposition and the rate of egg deposition will be increased.
2. Pre-bloom leaves will extend the life-span of the female leafhoppers to a significant degree. Senescent foliage and stems will assure for some time the survival of the insects. In this, the controlled experiments were in complete accord with the preliminary observations, which revealed that decadent vegetation did not foster egg deposition but could assure survival a rather long time after oviposition had ceased.
3. The common bean had a distinctly favorable effect on egg production, duration of oviposition, oviposition rate, and life-span.

Field observations reinforce these findings. Large numbers of nymphs and adults are common in bean fields.

Hardly any infestation occurs on cowpea plantings. The fact that cowpea does not harbor leafhoppers under field conditions is probably indicative that it lacks some attractant. This is further corroborated by the fact that this species allows survival and multiplication of leafhoppers under conditions of confinement. In other words, cowpea does not seem to contain any deterrent to leafhopper survival.

4. E. phaseola is able to survive on a rather diversified series of host plants.

The case of cowpea which is a mediocre to poor host for the leafhoppers in the field is puzzling. This plant species will sustain the insect when the latter is confined on it but will not favor its longevity nor its egg production. It seems logical that the reason may lie in the quality or abundance of some specific food elements. That nutrients may be limiting is suggested by the observation that leafhoppers may survive on nutriment obtained by feeding on the sap of damaged plants, practically devoid of green tissues. Under these circumstances the females do not oviposit and it is suspected that the eggs do not successfully mature. It is probable, however, that the interruption, even in extreme situations, does not reach the condition of oosorption, the follicle cells ceasing to participate in egg formation and the oocyte dying and being reabsorbed. This seems to be indicated by the strikingly

fast resumption of oviposition in females shifted from a deficient to an adequate host plant. Oogenesis and vitellogenesis would drain heavily on the female leafhoppers' reserves of proteins, nucleic acids, lipids, and glycogen. Replenishment would depend upon the quality of the food source.

5. Mating is largely governed by the age of the female leafhopper. The males are ready to copulate as early as 2 days after they have reached the adult stage. The females have to go through a period of maturation of at least 6 days. Interaction between the sexes was found to be insignificant, males and females mating successfully at all ages and giving rise to nymphs which develop normally.

   Since the males can mate several times, they can inseminate females not only of their own generation but of any of the overlapping generations in the bean field, a factor of great importance in the maintenance and increase of leafhopper populations.

6. Under the climatic, vegetational, and agricultural conditions prevailing in Costa Rica and throughout Central America, Empoasca phaseola Oman, therefore, quite successfully survives and reproduces in large numbers. As long as such crops as common beans and lima beans are cultivated in small home gardens, the damage by the insect will be important but not prohibitive. The situation can change drastically if large-scale

plantations are established, for example, for the purpose of exportation. The pest will no more be inconspicuous but will have to be recognized as one of outstanding importance.

SUMMARY

Empoasca phaseola Oman is a species of leafhopper found commonly in the more humid parts of the Central American area. It feeds on a wide variety of plants, both wild and cultivated, inflicting rather severe damage to its hosts.

Leguminous species are probably among its most suitable host plants. The interactions of E. phaseola with three species were studied. Striking differences were found in the damage caused by the insects and in the effect of the plants on the biology of the insect.

Common bean (Phaseolus vulgaris L.) proved to be the most favorable host, increasing the number of eggs deposited and extending the longevity of the pest. Next were lima bean (Phaseolus lunatus L.) and cowpea (Vigna sinensis Endl.). For practical reasons, wild host plants had to be surveyed only rapidly and not investigated in detail. There is no doubt that they play an important role in the maintenance of leafhopper populations in the absence of cultivated fields.

Incubation was found to last from 8 to 10 days. The average duration of nymphal development varied from 11 to 16 days depending on type of host or stage of maturity. No consistent difference was found between the sexes. Under the most favorable feeding conditions, inseminated females deposited eggs during 65 and 68 days and lived, in general from 83 to 96 days. The longest life-span recorded was on young common bean and lasted 219 days. The highest number of eggs deposited was 373. Daily oviposition rate on young bean foliage averaged 2.6 eggs, the highest rate being 4.74.

The study of the interactions of E. phaseola with some selected hosts in Central America seems to point to a set of conditions which favors perpetuation of E. phaseola as a potential threat to bean production. Should the present peasant agricultural pattern be changed to one of commercial exploitation, E. phaseola and many related species of Cicadellidae could become extremely important pests.

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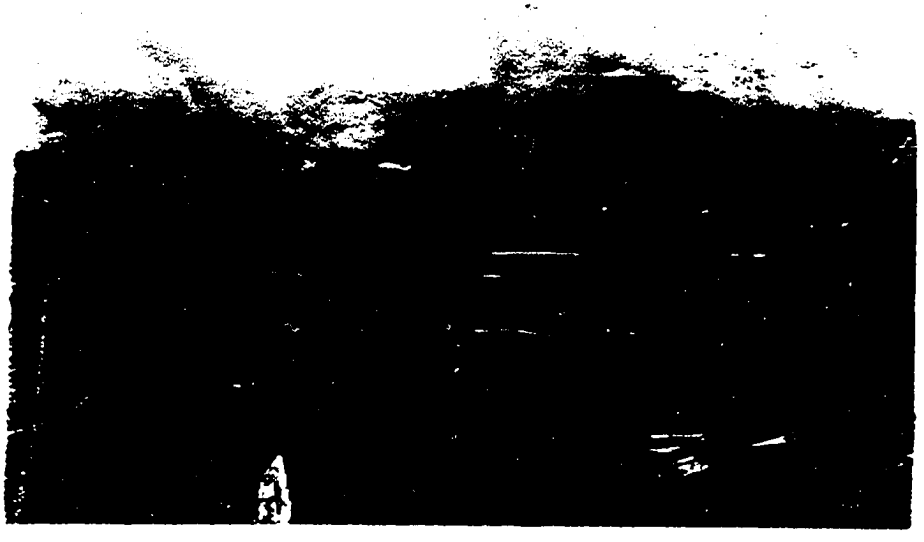
APPENDIX

Fig. 1 (Upper picture). Central Plateau (La Meseta Central) in Costa Rica. Sugarcane and coffee plantations, small orchards, and some banana clumps

Fig. 2 (Lower picture). Close-up of a field of common bean with voluntary corn and mixed weeds



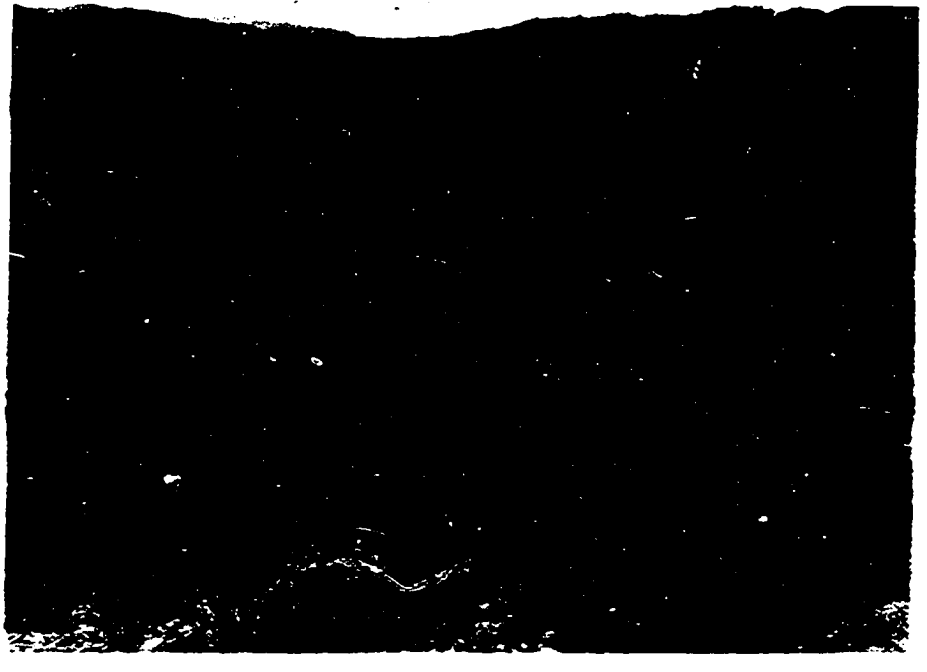


Fig. 3. Ecological map of Costa Rica adapted from L. R. Holdridge by J. A. Tosi, Jr. of the Tropical Science Center in San José, Costa Rica

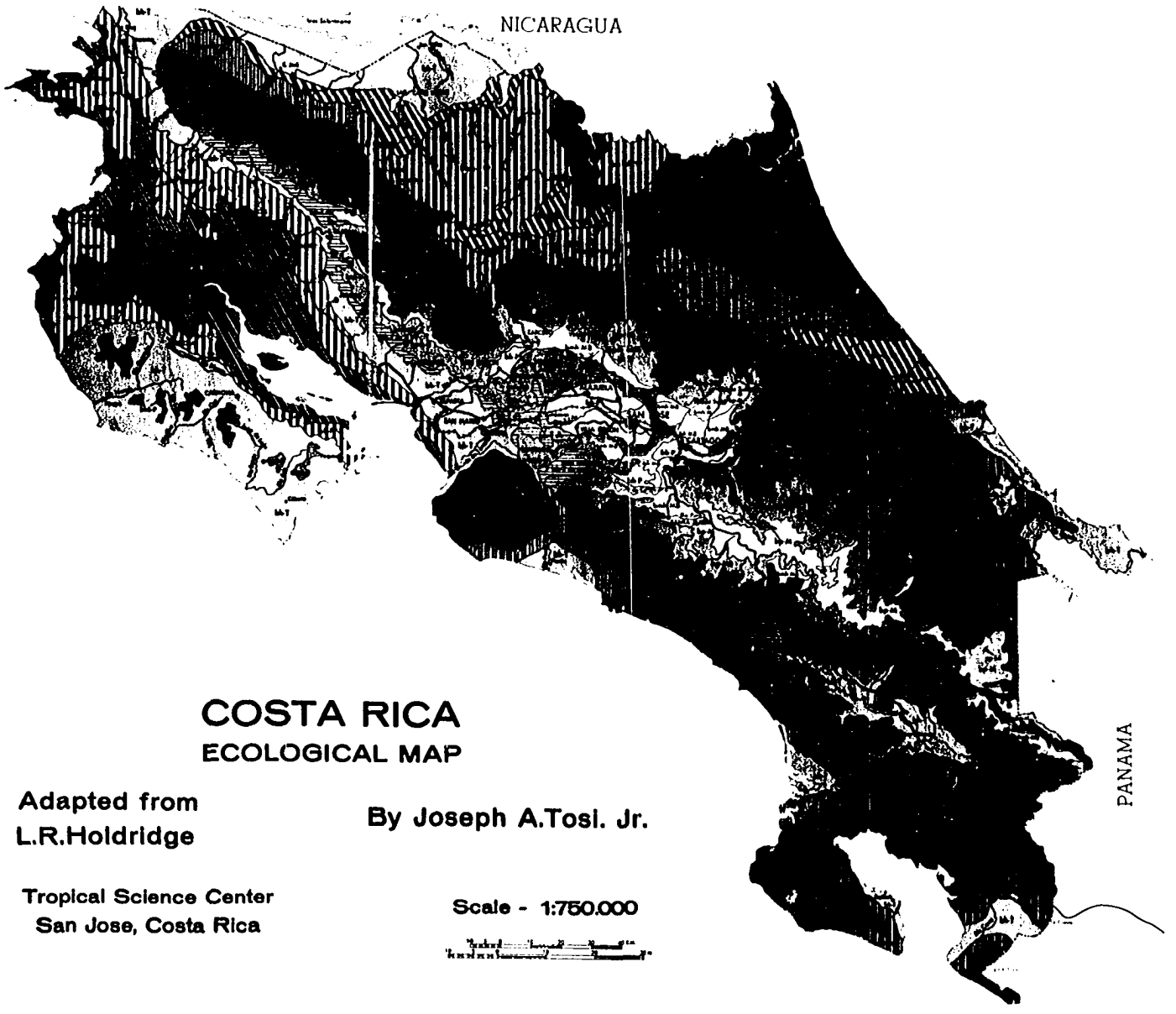

NICARAGUA
PANAMA
COSTA RICA
ECOLOGICAL MAP
Adapted from
L.R.Holdridge
By Joseph A.Tosi. Jr.
Tropical Science Center
San Jose, Costa Rica
Scale - 1:750.000

Fig. 4. Legend of Ecological map of Costa Rica (Fig. 3). Only the life zones where Empoasca leafhoppers were found are represented

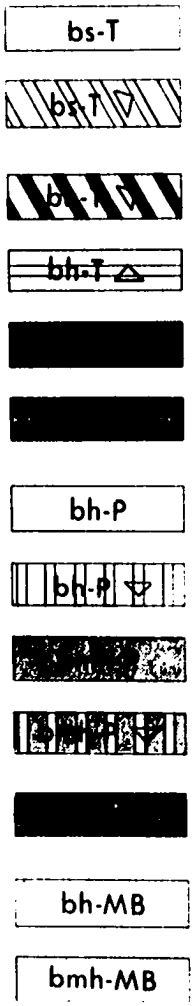

bs-T
Tropical dry forest
bs-T
Tropical dry forest, moist province transition
bh-T
Tropical moist forest, perhumid province transition
bh-T
Tropical moist forest, premontane belt transition
Tropical wet forest
Tropical wet forest, premontane belt transition
bh-P
Premontane moist forest
bh-P
Premontane moist forest, basal belt transition
Premontane wet forest
Very humid premontane, basal belt transition
Premontane rain forest
bh-MB
Lower montane moist forest
bmh-MB
Very moist forest, premontane

Fig. 5. Phylogenetic tree of the subgenus Empoasca as suggested by H. B. Cunningham (1962)

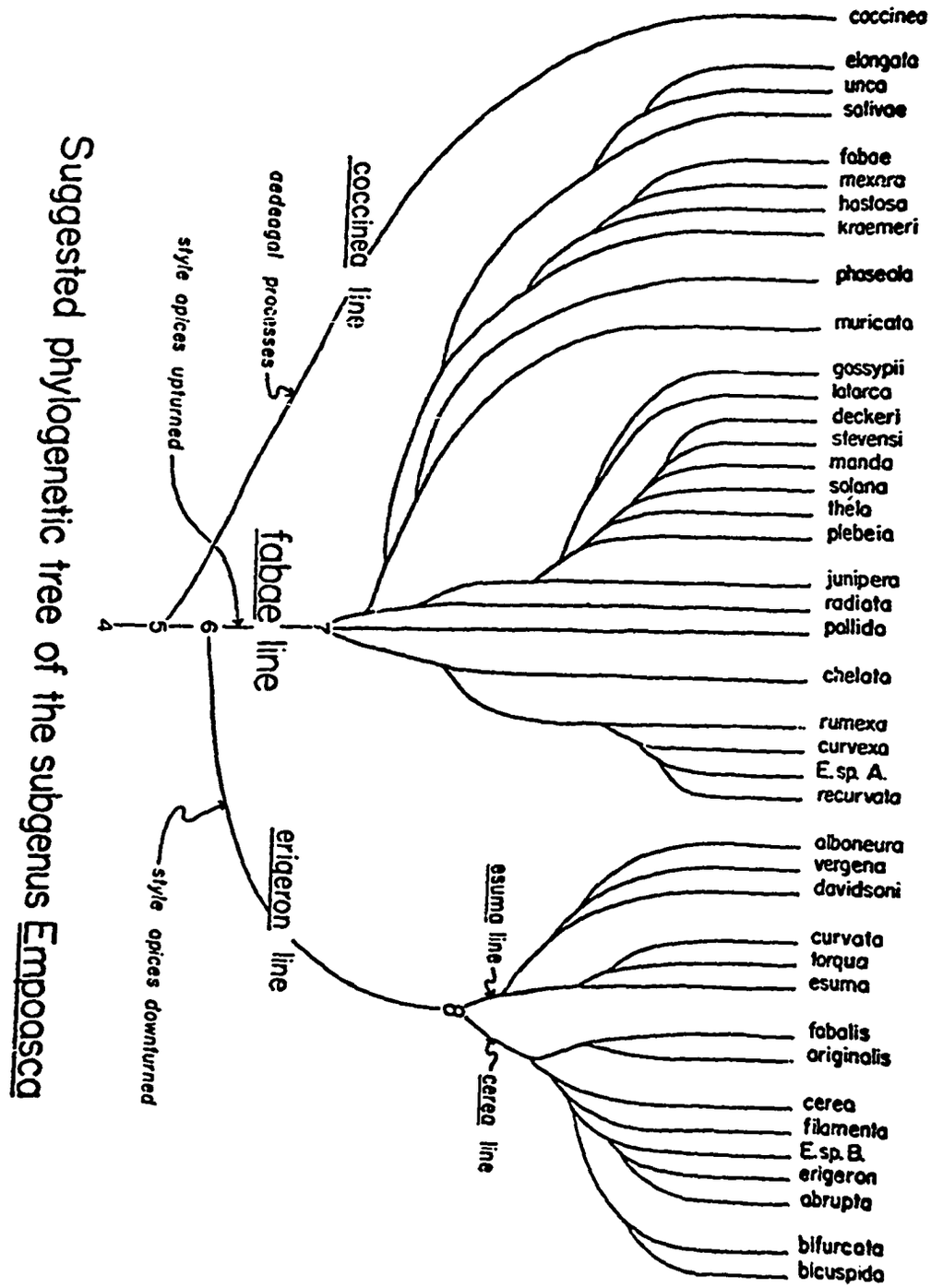

Suggested phylogenetic tree of the subgenus Empoasca
coccinea line
aedeagal processes
style apices upturned
fabae line
erigeron line
style apices downturned
esuma line
cerea line
4
5
6
7
8
coccinea
elongata
unca
salivae
fabae
mexana
hastosa
kraemeri
phaseola
muricata
gossypii
latarca
deckeri
stevensi
manda
solana
thela
plebeia
junipera
radiata
pallida
chelata
rumexa
curvexa
E. sp. A.
recurvata
alboneura
vergena
davidsoni
curvata
torqua
esuma
fabalis
originalis
cerea
filamenta
E. sp. B.
erigeron
abrupta
bifurcata
bicuspida

Fig. 6. Distribution of Empoasca in Central America

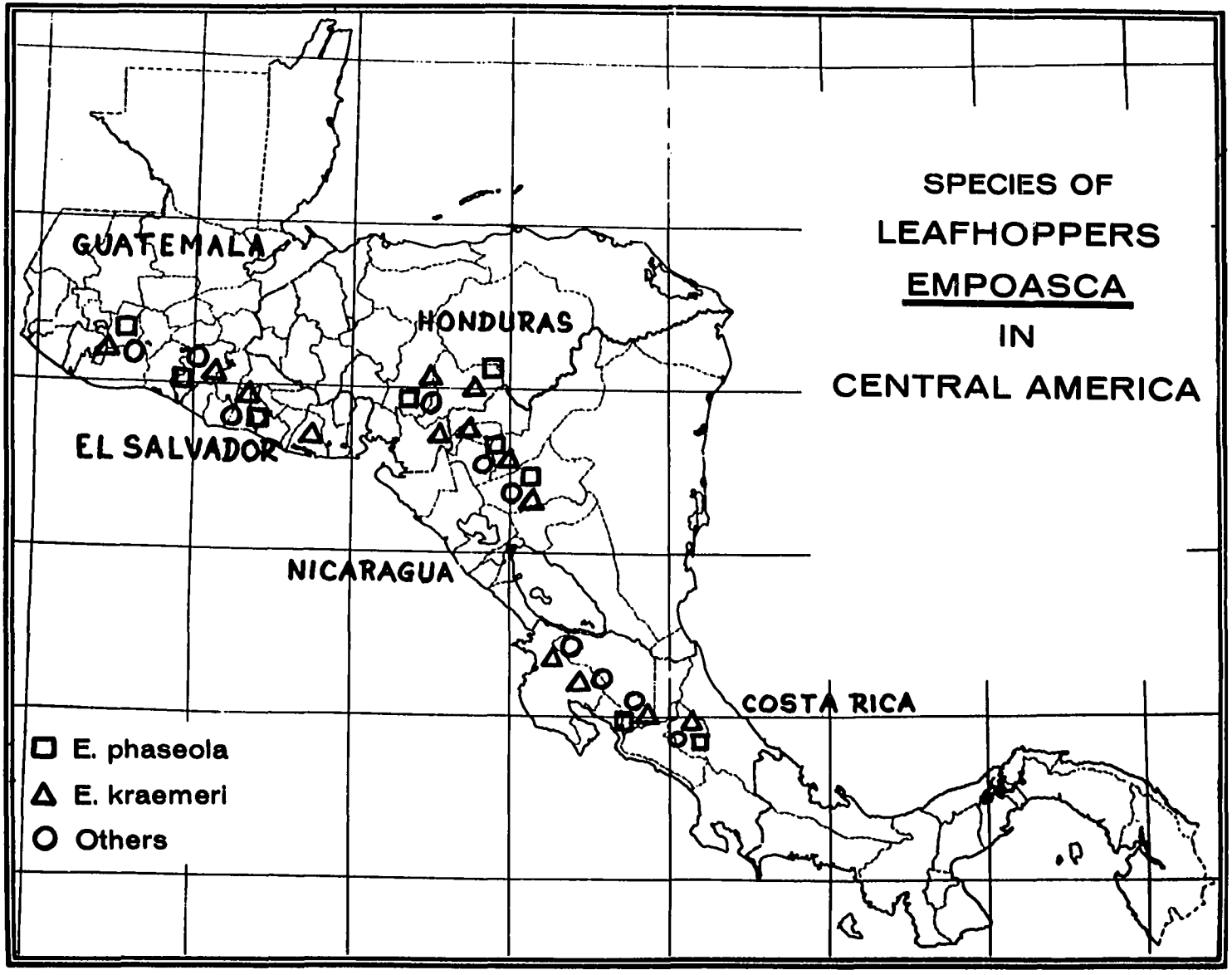

SPECIES OF
LEAFHOPPERS
EMPOASCA
IN
CENTRAL AMERICA
GUATEMALA
HONDURAS
EL SALVADOR
NICARAGUA
COSTA RICA
E. phaseola
E. kraemeri
Others

Fig. 7 (Upper picture). Clump of "Huitite" in Cartago, Costa Rica. The plants show symptoms of damage by E. phaseola. They are stunted and display considerable yellowing along the margins of their leaves

Fig. 8 (Lower picture). Close-up of the ornamental Solanum, Cestrum warscewiczii Klotzsch, very susceptible to damage by E. phaseola

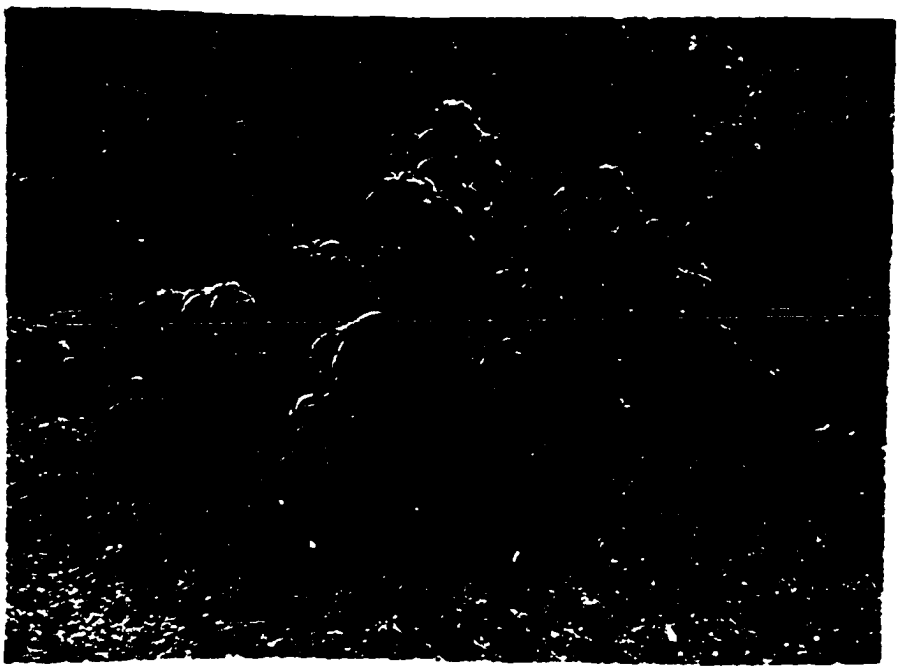


Fig. 9 (Upper picture). Screenhouse for the growing of clean plant material and the rearing of test insects at Turrialba Research Center (Costa Rica)

Fig. 10 (Lower picture). Lima bean plant recovering from heavy damage by *E. phaseola*

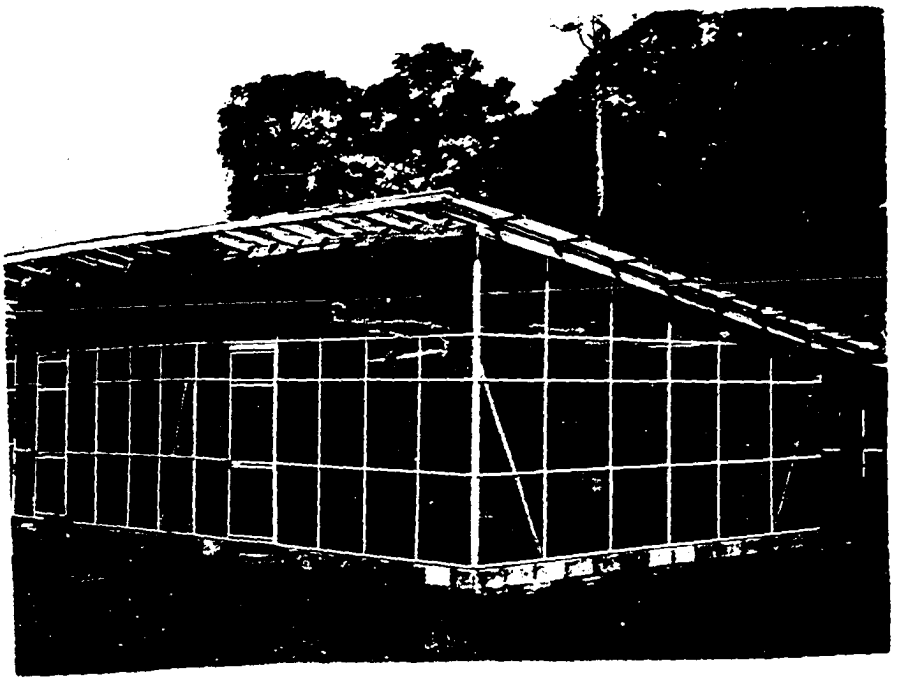


Fig. 11 (Upper picture). Phaseolus vulgaris growing in screenhouse at the Turrialba Research Center. The numbers on the side of the planting trough identify groups of plants sowed at intervals of 3 days

Fig. 12 (Lower picture). The 2-tube fluorescent desk lamp in the foreground provides light for cut leaves immersed in sucrose solution within Erlenmeyer flasks

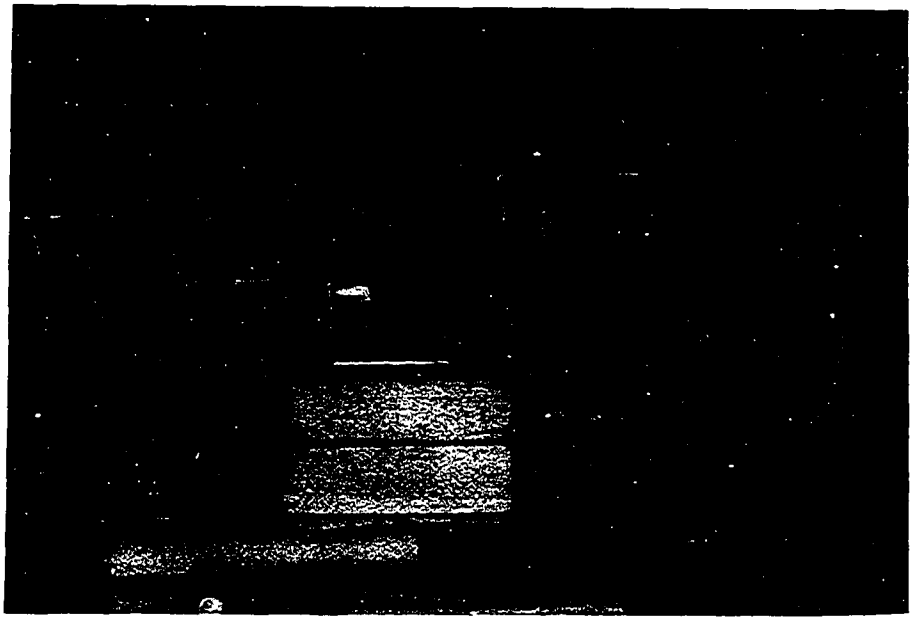


Fig. 13 (Upper picture). Cage for rearing E. phaseola in screenhouse at the Turrialba Research Center

Fig. 14 (Lower left picture). Phaseolus vulgaris of pre-bloom age

Fig. 15 (Lower right picture). Phaseolus vulgaris of post-bloom age

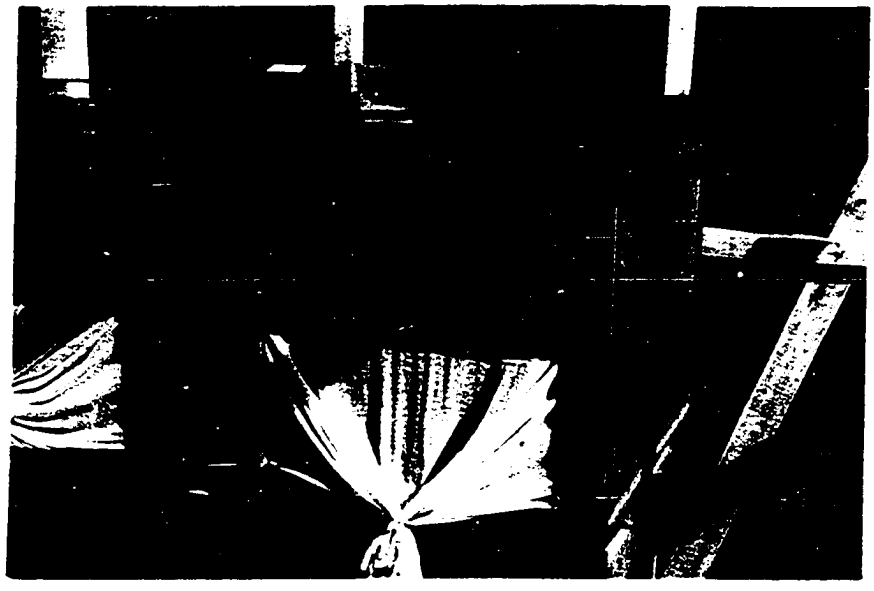


Fig. 16 (Upper picture). Potted cowpea plants in growth chamber

Fig. 17 (Lower picture). Bean petioles with leaves inserted through clear plastic snapboxes and immersed in sucrose solution. This setup was used in life-cycle studies of E. phaseola

Fig. 18 (Upper picture). Bean leaves damaged by E. phaseola. In the center is a healthy leaf. Advancing stages of the damage are presented in a clockwise manner beginning at the upper right

Fig. 19 (Lower picture). The upper 3 leaves display the typical damage by E. phaseola and the lower 3 the typical damage by E. kraemeri. The damage caused by the latter species is obviously more severe

Fig. 20 (Upper picture). Cut leaves of Phaseolus vulgaris immersed in 3% sucrose solution. This technique was used in rearing nymphs of leafhoppers to adults in the laboratory

Fig. 21 (Lower picture). Whole leaves inserted through plastic cages and fitted into waterpicks. This technique was used in Experiment I

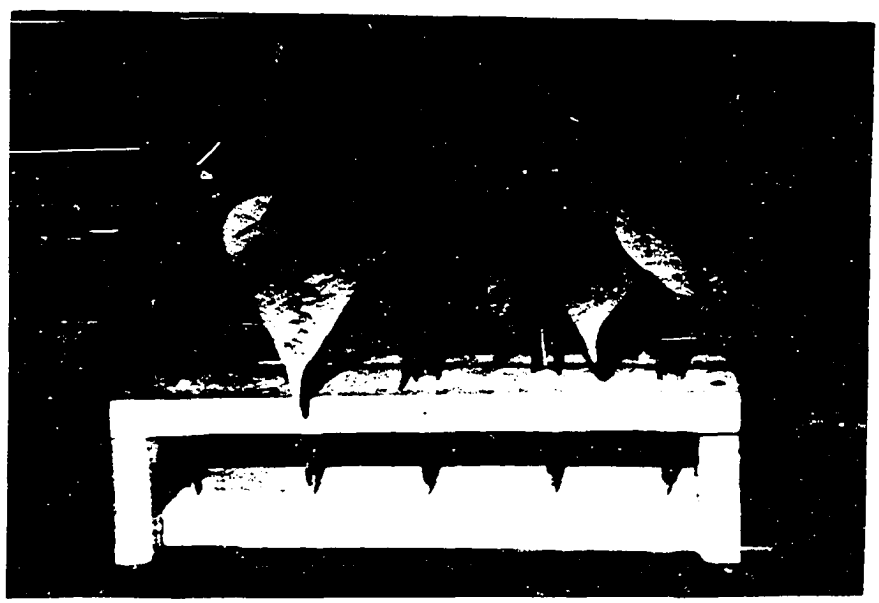


Fig. 22 (Upper picture). Whole bean leaves being mounted in aquapics across clear plastic snapboxes. On the lower left corner, an enamel pan fitted with hardware cloth for the transport of excised leaves from the screenhouse to the laboratory

Fig. 23 (Lower picture). Petiole change and cleaning of snapboxes within transfer cages. The construction of the latter can be seen: plastic top, saran-covered sides, sleeve of black cotton cloth, bottom lined with dark colored cardboard

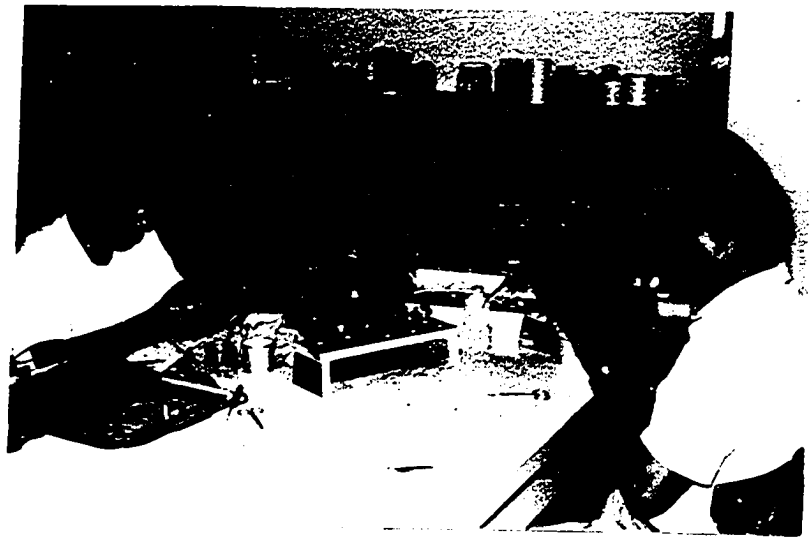
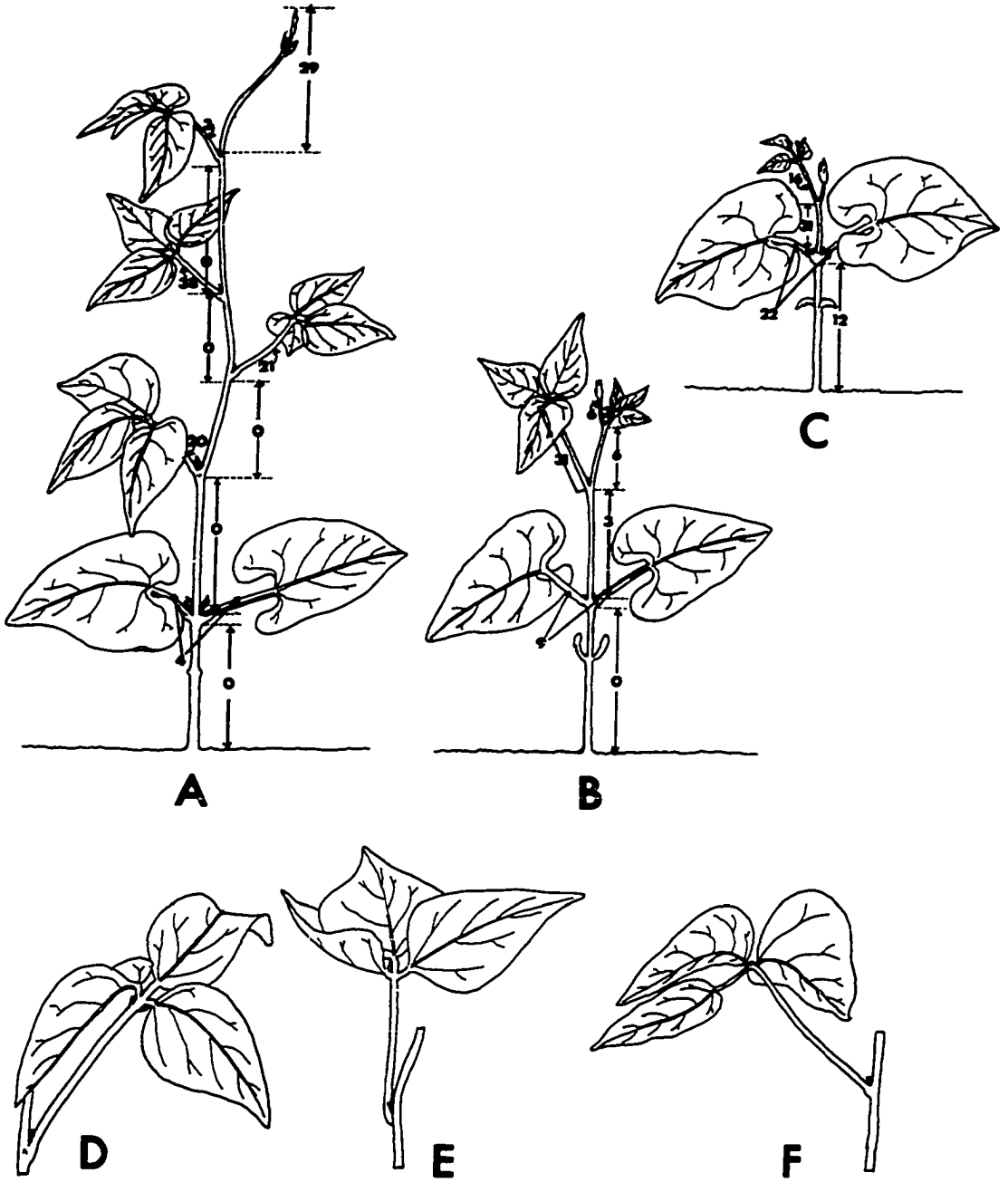


Fig. 24. Placement of eggs of E. phaseola within tissues of cowpea plants of different ages: A, B, and C are respectively 24, 15 and 12 days old. D, E, and F are typical leaves of cowpea, common bean and lima bean; the latter has the median petiolule significantly longer.


A
B
C
D
E
F

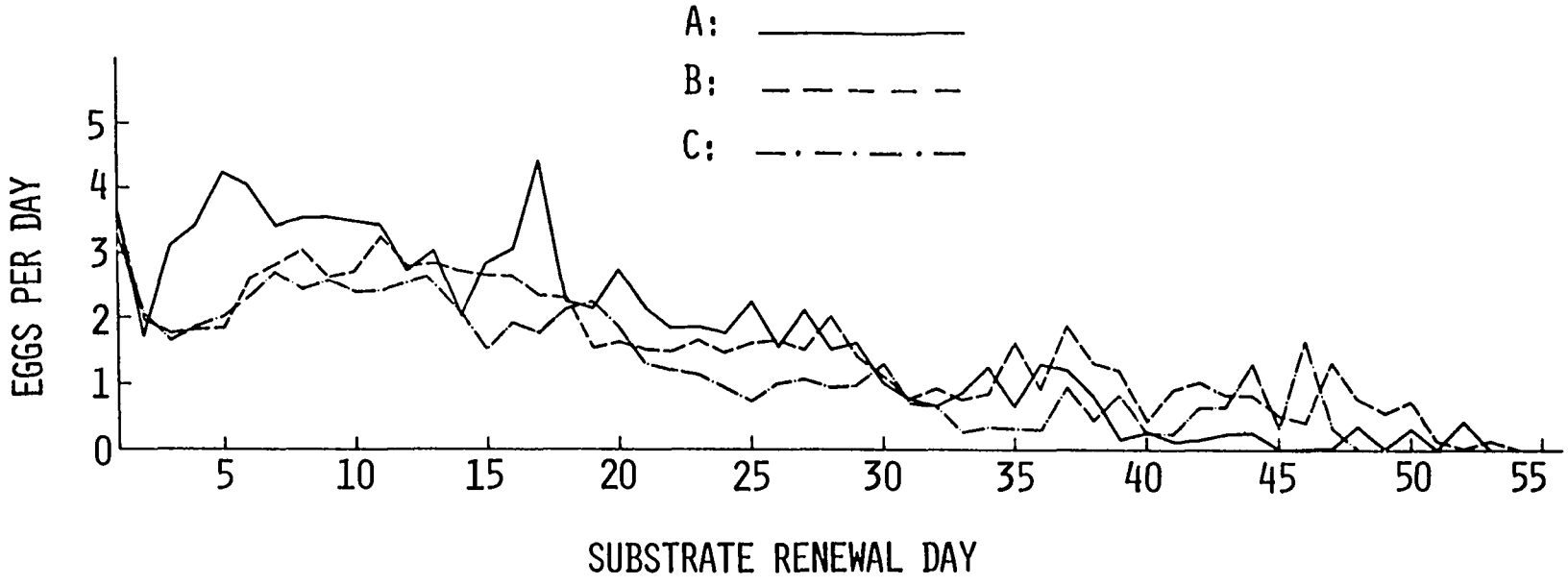


Fig. 25. Average daily rate of oviposition of E. phaseola on common bean Phaseolus vulgaris L. of 2 different stages of maturity

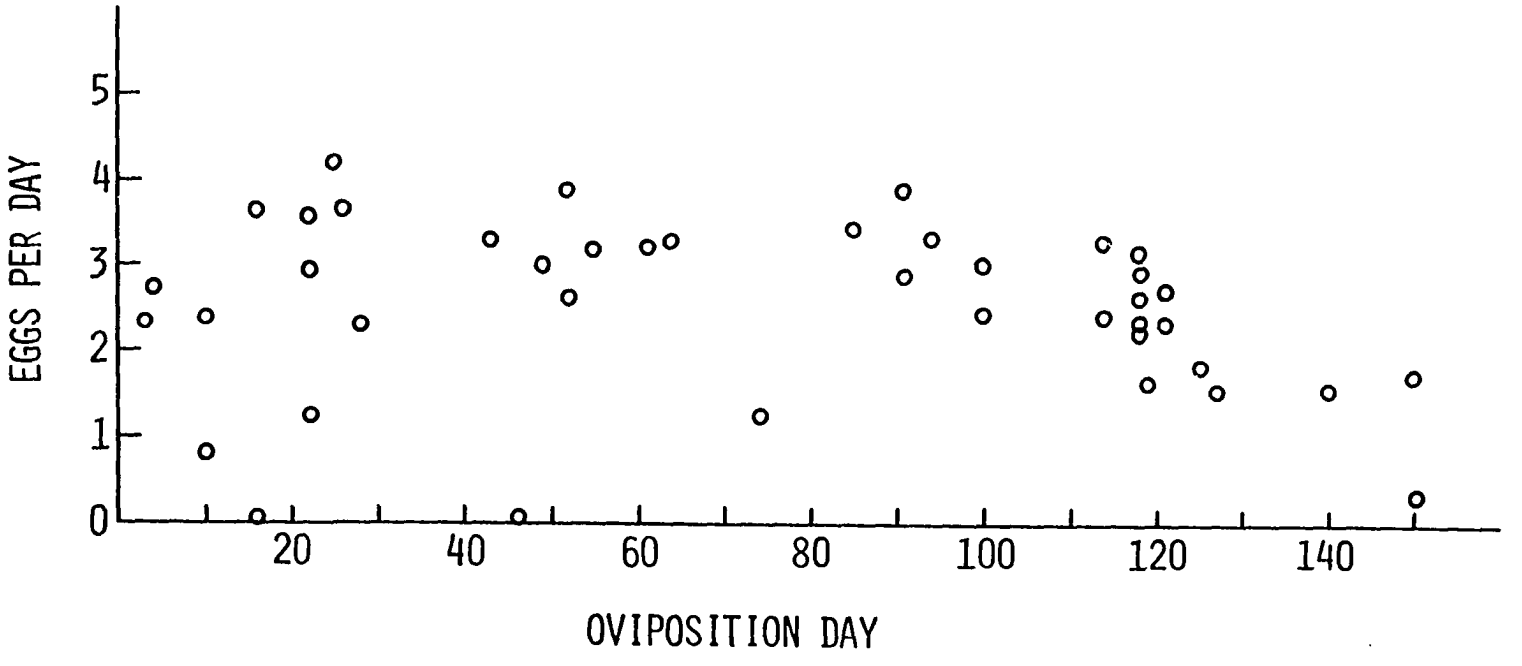


Fig. 26. Overall oviposition rate of females held continuously on pre-bloom leaves of common bean

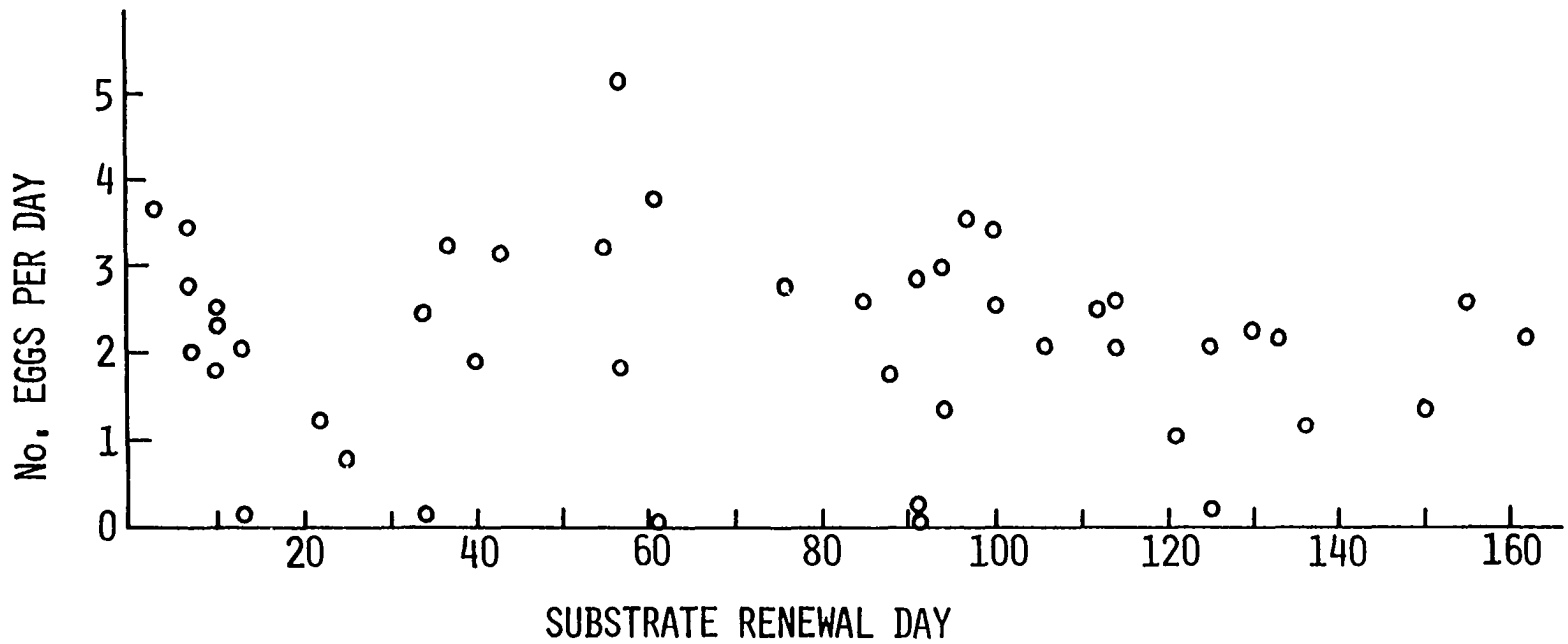


Fig. 27. Overall oviposition rate of females started on post-bloom leaves and transferred after 30 days to pre-bloom leaves of common bean

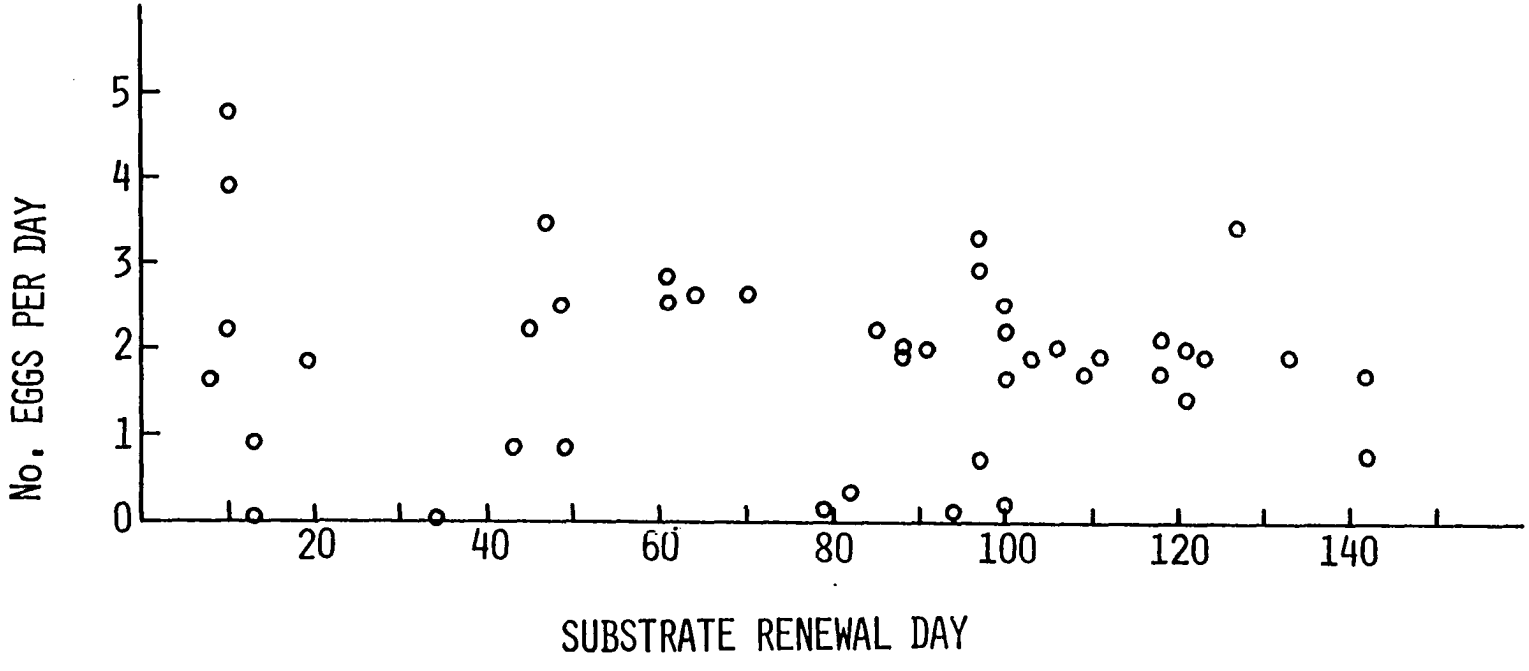


Fig. 28. Overall oviposition rate of females held continuously on post-bloom leaves of common bean

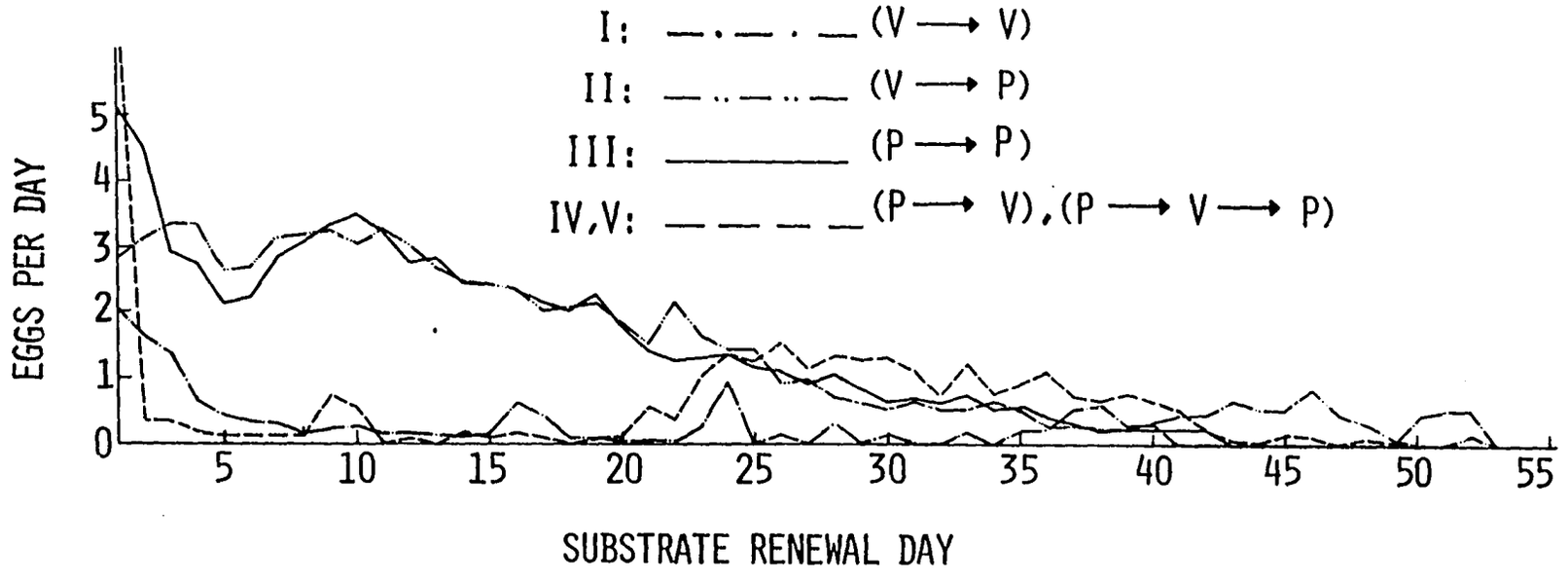


Fig. 29. Average daily oviposition rate of E. phaseola on common bean (P) and cowpea (V)

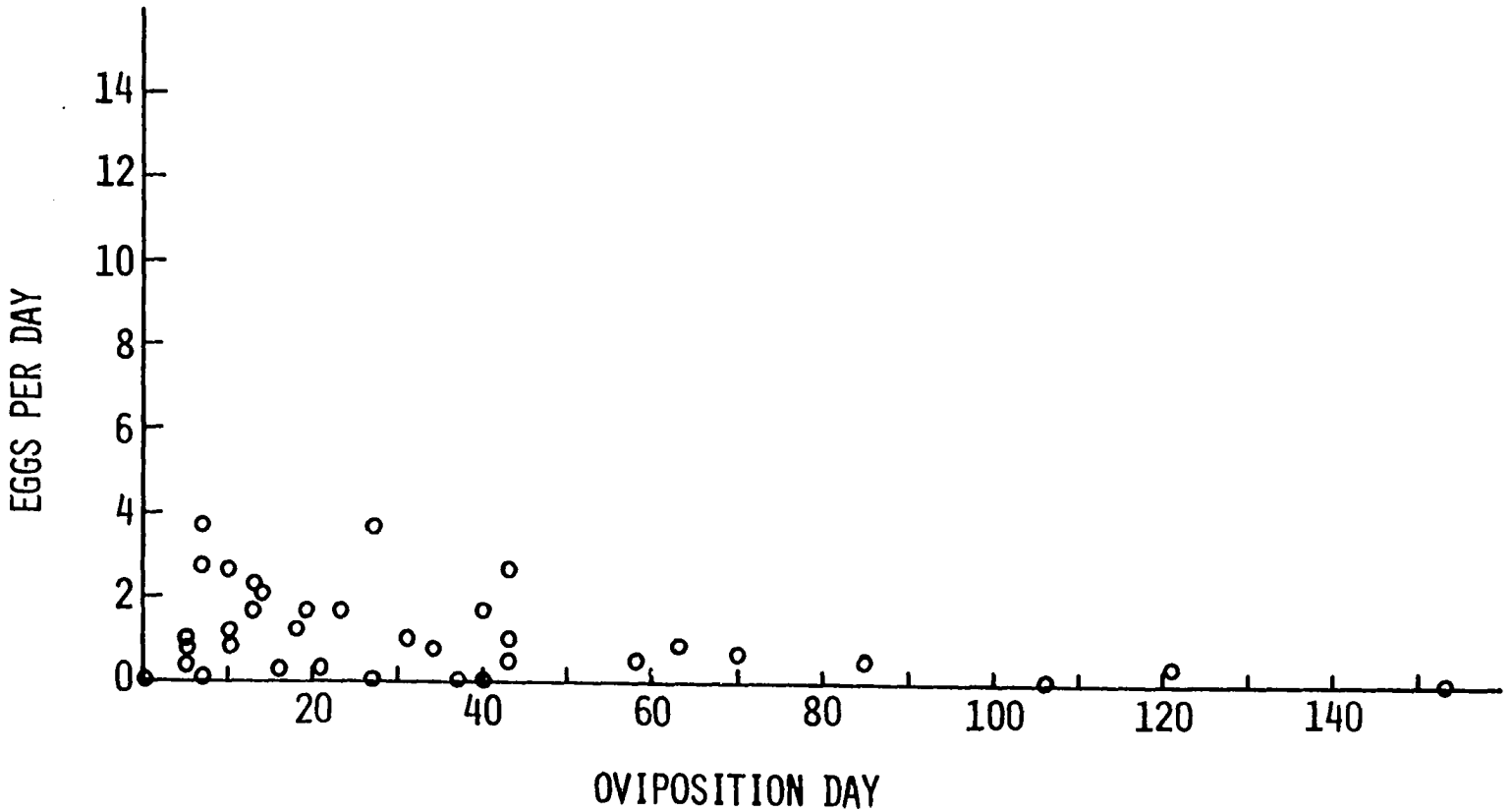


Fig. 30. Overall oviposition of females reared continuously on cowpea

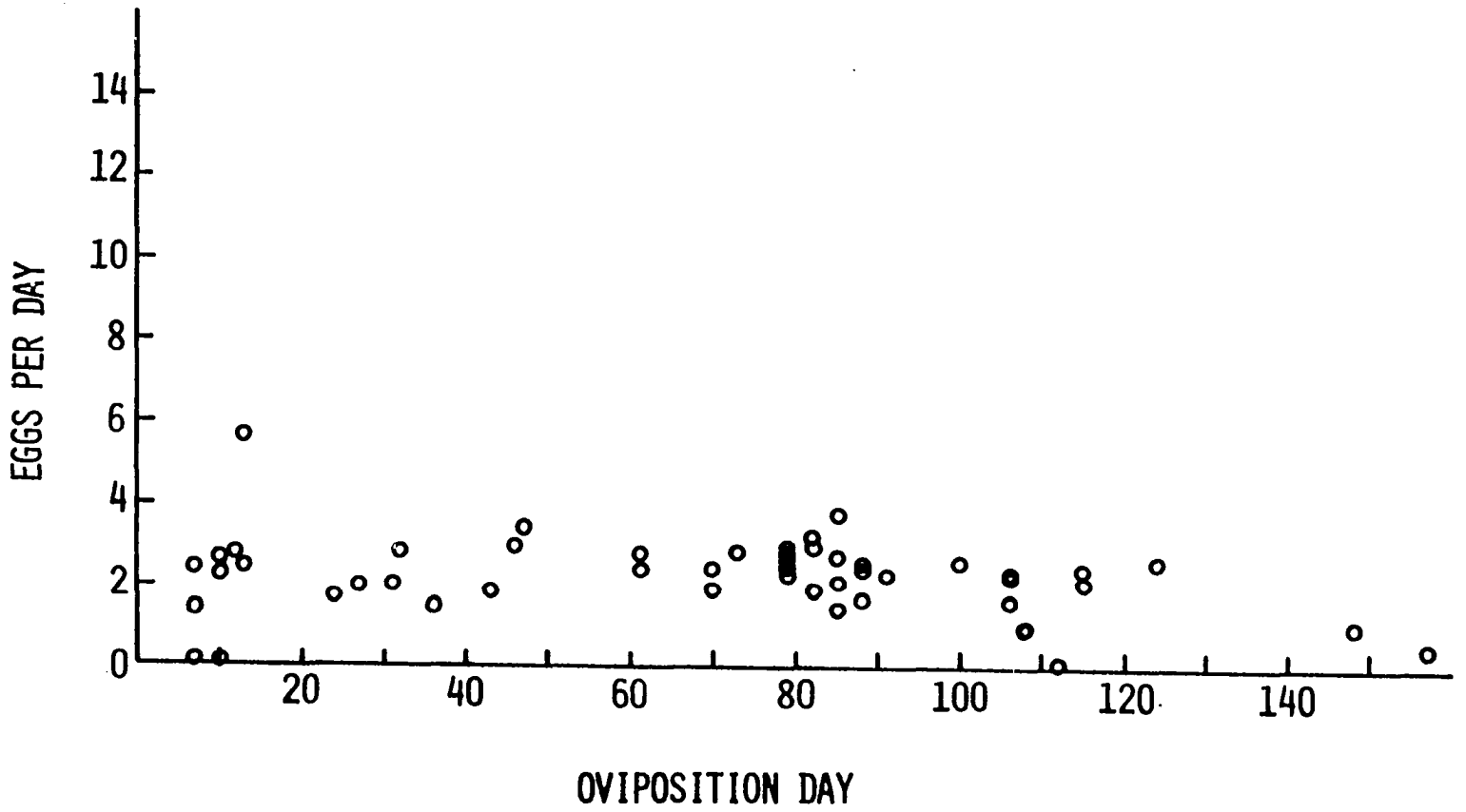


Fig. 31. Overall oviposition rate of females reared on cowpea and transferred to common bean

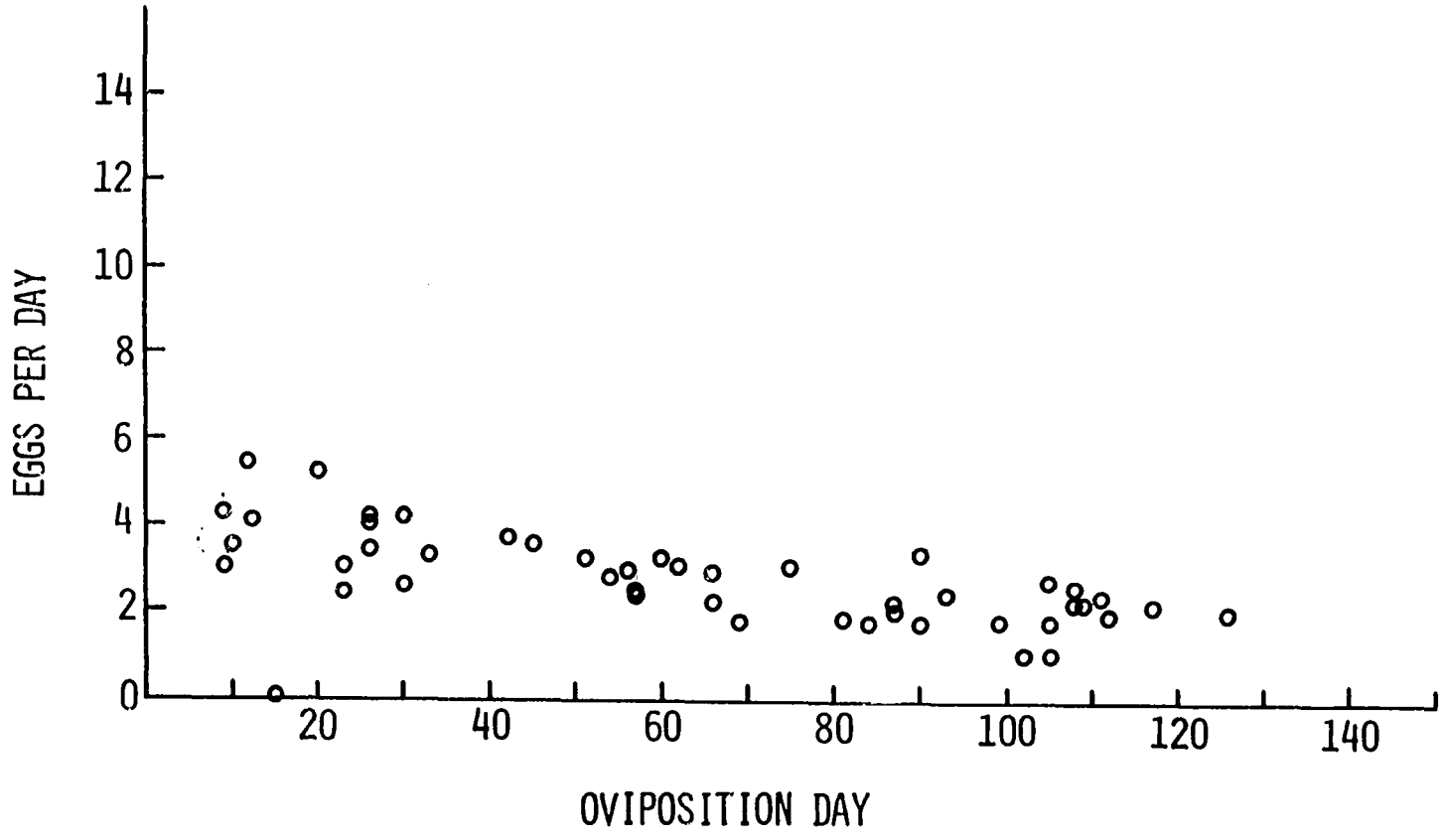


Fig. 32. Overall oviposition rate of females held continuously on common bean

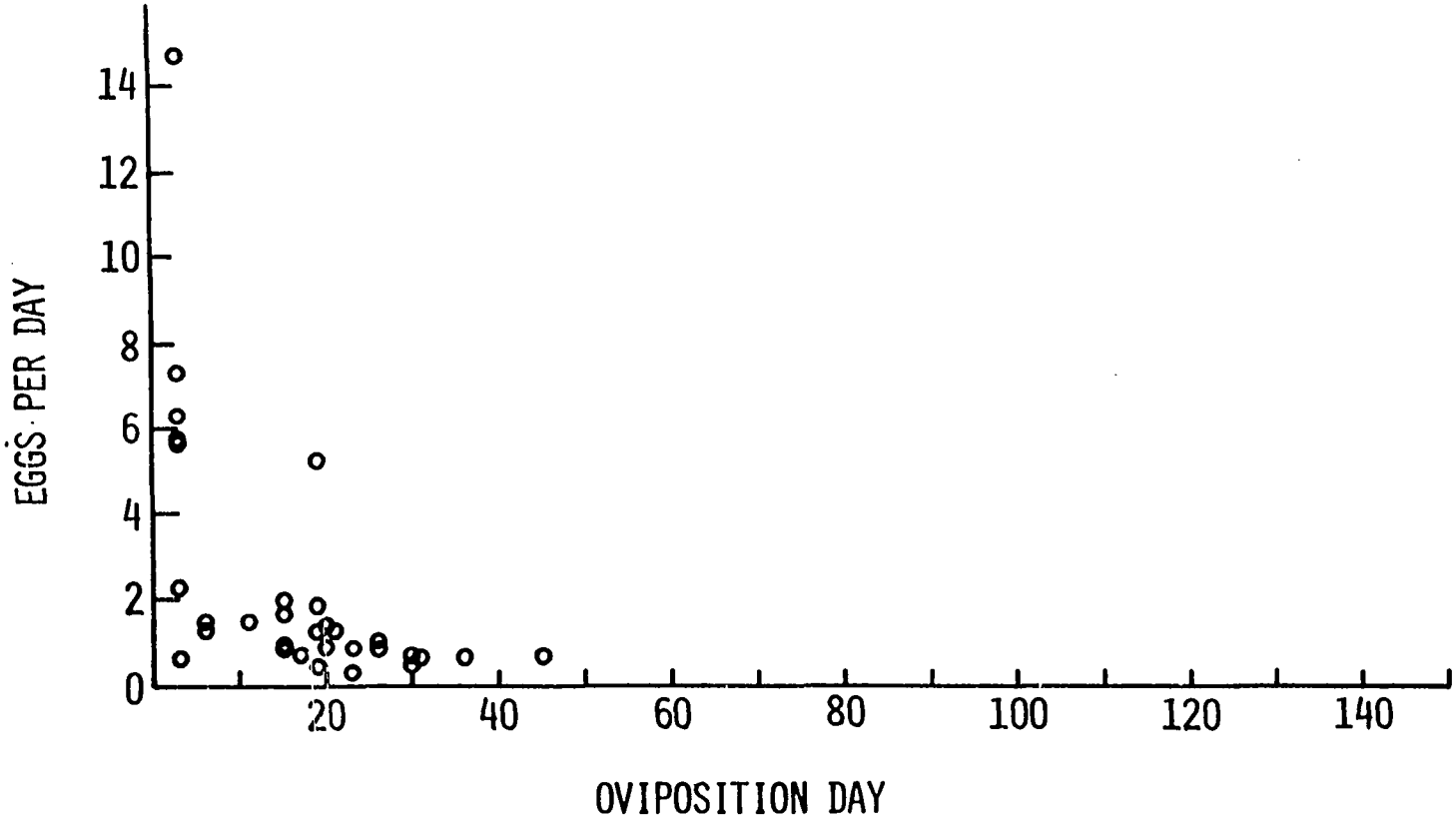


Fig. 33. Overall oviposition rate of females reared on common bean and transferred to cowpea after 30 days

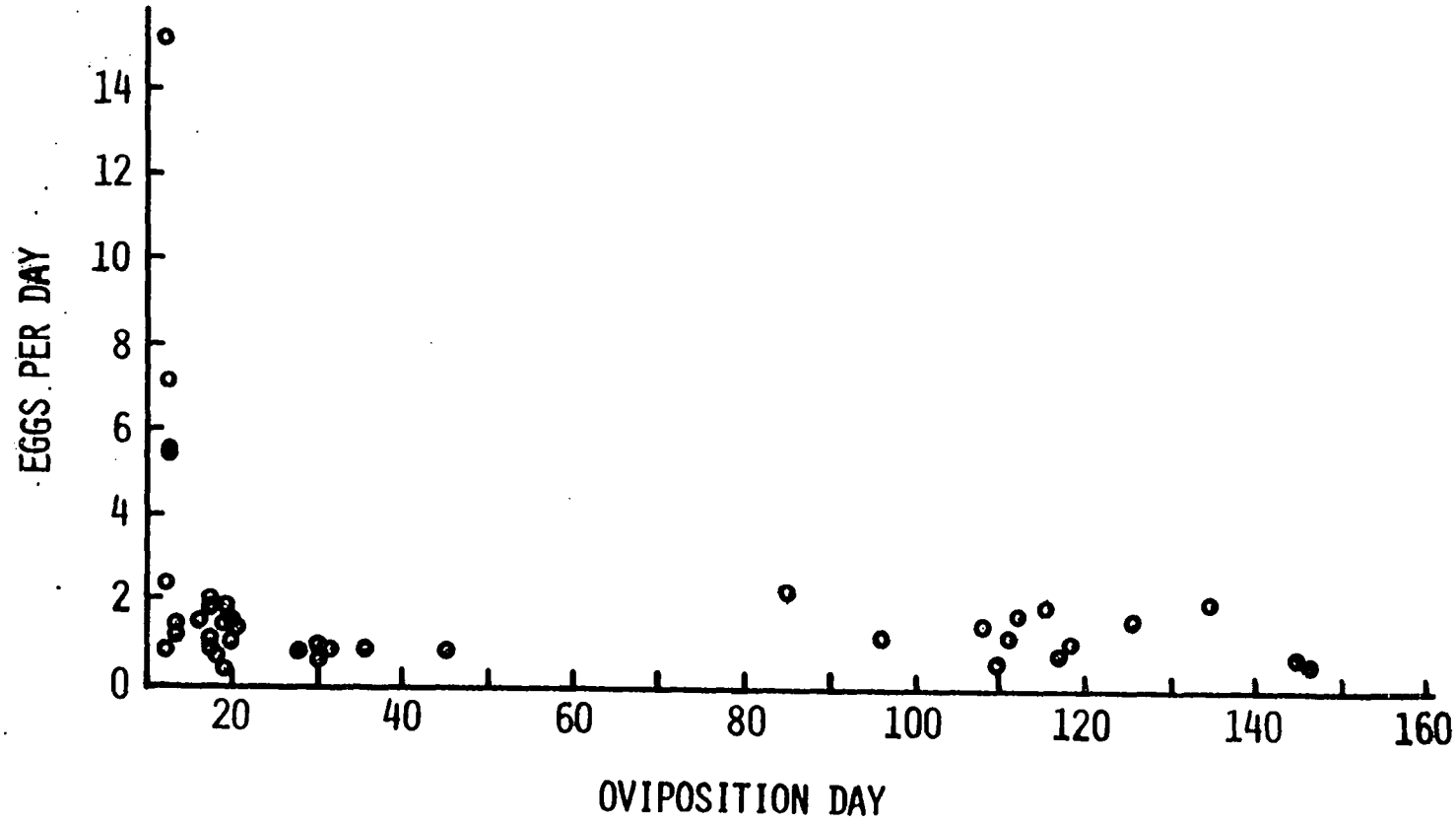


Fig. 34. Overall oviposition rate of females reared on common bean, transferred to cowpea, and returned to common bean at 81 days